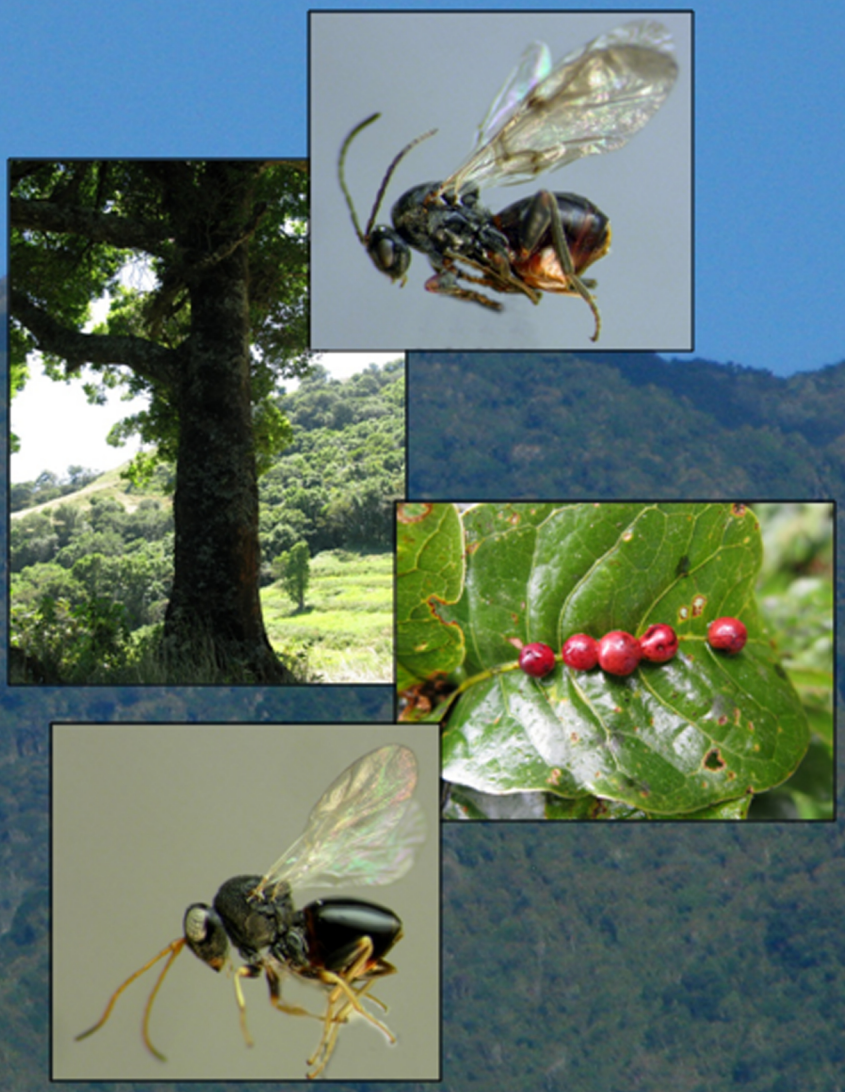
UNIVERSIDAD AUTÓNOMA DE MADRID

FACULTAD DE CIENCIAS
DEPARTAMENTO DE BIOLOGÍA

TAXONOMÍA Y BIOLOGÍA DE LOS CINÍPIDOS INDUCTORES DE AGALLAS E INQUILINOS (HYMENOPTERA, CYNIPIDAE) ASOCIADOS A ESPECIES DE *QUERCUS* (FAGACEAE) EN PANAMÁ



ENRIQUE MEDIANERO SEGUNDO

MADRID, 2011

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Tesis Doctoral

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Memoria presentada por **ENRIQUE MEDIANERO SEGUNDO** para optar al grado de Doctor en Ciencias Biológicas

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VºBº Director de tesis

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Madrid, 2011

El Doctor José Luis Nieves Aldrey, del Departamento de Biodiversidad y Biología Evolutiva del Museo Nacional de Ciencias Naturales (CSIC),

HACE CONSTAR:

Que la Tesis Doctoral titulada "**Taxonomía y Biología de los cinípidos inductores de agallas e inquilinos (Hymenoptera, Cynipidae) asociados a especies de *Quercus* (Fagaceae) en Panamá**" presentada por Enrique Medianero Segundo para optar al grado de doctor en ciencias biológicas en la Universidad Autónoma de Madrid, ha sido realizada bajo su dirección.

Y para autorizar su presentación y evaluación por el tribunal correspondiente, firma la presente a 01 de marzo de 2011.

Vº Bº Director de la Tesis

Fdo. Dr. José Luis Nieves Aldrey

Enrique Medianero Segundo

A mis hijos: Gabriel y Liseth

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ÍNDICE

INTRODUCCIÓN

CYNIPOIDEA Y CYNIPIDAE: LOS CYNIPIDAE DE LA REGIÓN NEOTROPICAL Y DE PANAMÁ

Los Cynipoidea constituyen una de las principales superfamilias del orden Hymenoptera, con más de 3.000 especies conocidas, incluidas en 223 géneros. Es, después de *Ichneumonoidea*, *Chalcidoidea* y *Proctotrupoidea* (*sensu lato*), el grupo de himenópteros más numeroso en especies a escala mundial (Nieves-Aldrey, 2001). La superfamilia aún está relativamente poco estudiada, sobre todo los grupos tropicales, y probablemente una importante fracción de las especies de la fauna de estos insectos todavía no se ha descrito (Nieves-Aldrey, 2001). La vasta mayoría de los Cynipoidea son avispas pequeñas con longitudes de 1.0 hasta 6.0 milímetros, aunque unas pocas especies que parasitan barrenadores de madera pueden alcanzar los 30 milímetros. Se trata de insectos de colores por lo general sombríos, negros, rojizos, ambarinos o castaños, brillantes o mates pero nunca con las tonalidades metálicas que presentan otros Hymenoptera (Nieves-Aldrey, 2001). Entre las autapomorfias propuestas para esta superfamilia se pueden señalar: base de escapo antenal desprovisto de radícula (caso único entre los Hymenoptera); ala anterior desprovista de vena costal (C) (ausente también en el diseño ancestral de Chalcidoidea); ala anterior con vena medial (M) desplazada hacia la parte anterior próxima al extremo posterior de la celda marginal; metasoma lateralmente muy comprimido (al igual que en el diseño ancestral de Evaniidae, Austroniidae, y posiblemente de Roproniidae); esternos metasomales I y II adosados o fusionados (Ronquist, 1999, 2006).

La filogenia de la superfamilia ha sido analizada en varios trabajos recientes (Ronquist, 1994, 1995a, 1995b, 1999; Nordlander *et al*., 1996; Liljeblad & Ronquist, 1998; Ros-Farré *et al*., 2000; Liu, 2001; Fontal-Cazalla *et al*., 2002; Nylander *et al*., 2004; Liljeblad *et al*., 2008; Nieves-Aldrey *et al.,* 2009) sin embargo muchas relaciones evolutivas entre los diferentes grupos de Cynipoidea aun están por resolver. Siguiendo la clasificación de Ronquist (1995b, 1999) se admiten que en el ámbito mundial la superfamilia comprende cinco familias actuales: Austrocynipidae (incluyendo un sólo género monotípico de Australia), Liopteridae (10 géneros y 170 especies, especialmente tropicales), Ibaliidae (un género y 19 especies de la región Holártica), Cynipidae (77 géneros y unas 1400 especies, principalmente holárticas) y Figitidae (130 géneros y 1400 especies en todo el mundo) (Ronquist, 2006).

Los Cynipoidea se pueden dividir en “macrocinipoideos” y “microcinipoideos” basándose en la talla y algunos rasgos morfológicos típicos (Ronquist, 1995b). Un análisis filogenético basado en caracteres morfológicos de los adultos señala que los

microcinipoideos son monofiléticos y que los macrocinipoideos constituyen un conjunto parafilético que agrupa los linajes cinipoideos basales, en los que Austrocynipidae sería el grupo hermano de los demás Cynipoidea (Ronquist, 1995b) (Fig. 1A). En general, los macrocinipoideos (Austrocynipidae, Ibaliidae y Liopteridae) son insectos relativamente grandes que parasitan larvas de insectos barrenadores de madera, ramas y conos fructíferos de gimnospermas. Este grupo de cinipoideos pupan en el interior de un sustrato duro y los adultos tienen que excavar una galería u orificio para poder emerger. Por esta razón son insectos largos, de talla relativamente grande y tegumentos fuertemente esclerotizados, a la vez que presentan los rasgos típicos de los barrenadores: patas gruesas y mandíbulas robustas, y una serie de estructuras que facilitan el avance en el interior de los túneles; crestas transversales en el mesosoma y, a veces, proyecciones tarsales muy evidentes (Fig. 1B). Los microcinipoideos (Cynipidae y Figitidae), en cambio tienden a ser de menor talla, el mesosoma es más alto y compacto, y el metasoma mucho más corto, tanto que las alas se proyectan más allá del extremo posterior del cuerpo (Fig. 1C y 1D). Su cuerpo parece haber sido diseñado para pupar en una cámara esférica, en un sustrato más blando como una agalla o materia en descomposición. La parte dorsal del mesosoma suele carecer de crestas transversales y las patas son más delgadas y débiles que la de los macrocinipoideos (Ronquist, 2006). Al igual que los macrocinipoides los Figitidae son parasitoides y la mayor parte de las especies atacan larvas del orden Diptera, casi siempre larvas que se desarrollan en el interior de una planta o en un sustrato orgánico en descomposición. Varios linajes figítidos parasitan hospedadores asociados a Aphidoidea o a Psylloidea mientras otros se desarrollan dentro de agallas, pero lo más probable es que lo hagan como parasitoides de larvas de himenópteros cecidógenos (Ronquist, 1994; Ronquist & Nieves-Aldrey, 2001). La excepción al tipo de vida parasitoide dentro del seno de Cynipodea está singularizada por la amplia familia Cynipidae cuyos miembros son todos fitófagos especializados, inductores de agallas (cecidias) vegetales o inquilinos en las mismas. Aunque se han encontrado evidencias recientes de que el grupo pudiese incluir también especies que se comportan como parasitoides (Nieves-Aldrey *et al.,* 2009).

De las 10 familias del orden Hymenoptera capaces de inducir agallas los Cynipidae son los más diversos, siendo superados dentro de la Clase Insecta solo por los dípteros de la familia Cecidomyiidae. Las agallas inducidas por los cinípidos están consideradas entre las más diversas y complejas de todos los organismos capaces de

inducir agallas en la naturaleza (Askew, 1984; Nieves-Aldrey, 2001; Stone *et al*., 2002; Csóka *et al.,* 2005). Las especies inductoras de agallas de la familia Cynipidae junto con sus comunidades de inquilinos constituyen el objeto de estudio de esta tesis doctoral.

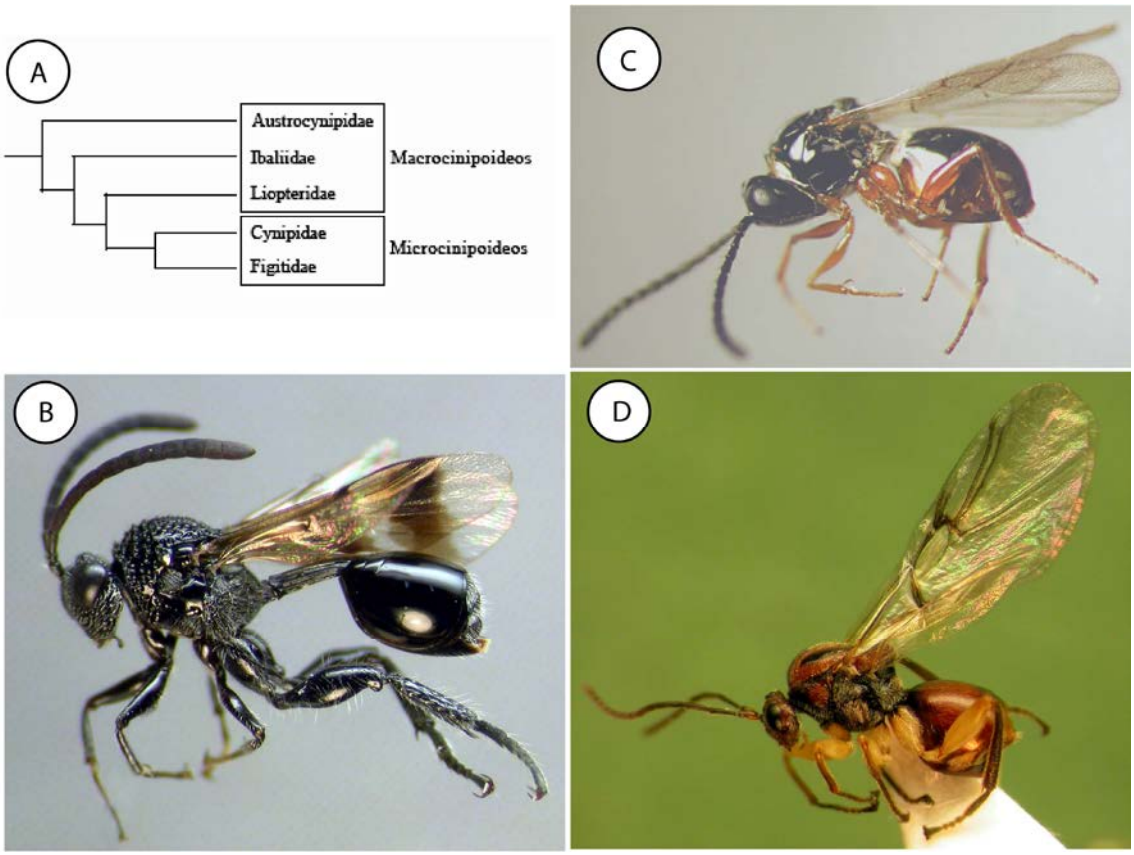

Figura 1. Relaciones evolutivas y habitus de los Cynipoidea: (A) Cladograma mostrando las relaciones filogenéticas de los Cynipoidea actualmente aceptadas, tomado de Ronquist 1995b. (B) Habitus de *Ibaliidae*, macrocinipoideo. C-D; Habitus de microcinipoideos; (C) Figitidae. (D) Cynipidae.

La familia Cynipidae

Los Cynipidae parecen ser un grupo monofilético hermano de Figitidae (Ronquist, 1994, 1995b, 1999) de los cuales en ausencia de información biológica pueden ser difíciles de separar. En general los cinípidos son insectos de talla pequeña o mediana (entre 1-6 mm), de coloración variable, aunque nunca metálica. Antenas con 12-15 segmentos (rara vez con 16); el tercer segmento (F1) suele estar modificado en los machos. Placa pronotal y carenas laterales del pronoto por lo general ausentes o indistintas. Mesosoma usualmente ornamentado y por lo general con los notaulos más o menos marcados. Tibias medias y posteriores con dos espolones cada una. Alados (raramente braquípteros o ápteros); ala anterior con la parte basal de la vena Rs+M

(cuando visible) dirigida hacia un punto medio de la vena basal. Metasoma nunca con anillo de pubescencia en el terguito III, el cual es grande y cubre gran parte del metasoma, aunque hay excepciones o los terguitos III y IV están fusionados, hipopigio normalmente prolongado ventralmente en una proyección apical denominada espina hipopigial (Pujade-Villar & Hanson, 2006).

Varias sinapomorfias han sido propuestas para la monofilia de Cynipidae, incluyendo la celda marginal del ala anterior abierta anteriormente, la ausencia de la carena pronotal lateral, y el área dorsal pronotal completamente ausente u oculta por el mesoescudo (Liljeblad & Ronquist, 1998; Ronquist, 1999). Sin embargo, todas las sinapomorfias morfológicas propuestas presentan excepciones en forma de reversiones secundarias dentro de los Cynipidae o estructuras paralelas en Figitidae (Liu & Ronquist, 2006). Ronquist (1999), sugiere que la presencia de dos dientes fuertes y romos en las mandíbulas del último estadio larval, puede ser la única sinapomorfia de Cynipidae (los figítidos parasitoideos y macrocinipoideos tienen solamente un diente agudo y fuerte). Esto está ampliamente confirmado en un estudio reciente de las mandíbulas larvales de Cynipoidea (Nieves-Aldrey *et al.*, 2005), aunque algunas larvas cinípidas han perdido el segundo diente; el diente principal es consistentemente más fuerte y más romo en las avispas que forman agallas que en sus vecinas parasitoides de insectos. En adición a las sinapomorfias propias de los cinípidos, hay un gran número de caracteres que son útiles para la separación de cinípidos y figítidos. Por ejemplo, la mayoría de los Figitidae tienen un mesoscudo liso y brillante (excepciones en Parnipinae, algunos Thrasorinae y Charipinae, *Melanips* [Figitinae] y Aspicerinae) mientras casi todos los cinípidos presentan un mesoescudo opaco debido a su microescultura coriácea. Los cinípidos inductores de agallas tienen típicamente una celda marginal abierta mientras la mayoría de cinípidos inquilinos y muchos Figitidae tienen la celda marginal cerrada. La mayoría de los cinípidos carecen de la carena lateral pronotal, siendo la excepción más notable el complejo de inquilinos *Synergus* de la región paleártica; con frecuencia, la placa pronotal anterior de los cinípidos está incompletamente definida en su parte lateral o incluso ausente (muchos inductores de agallas en plantas herbáceas y arbustos, avispas de las agallas en robles) pero cuando está completamente definida (inquilinos y muchos inductores de agallas en herbáceas), ésta nunca se levanta por encima del resto del pronoto. Figitidae tiene frecuentemente una carena pronotal lateral prominente o una placa pronotal bien definida y fuertemente

resaltada (emargininos y eucoilinos).

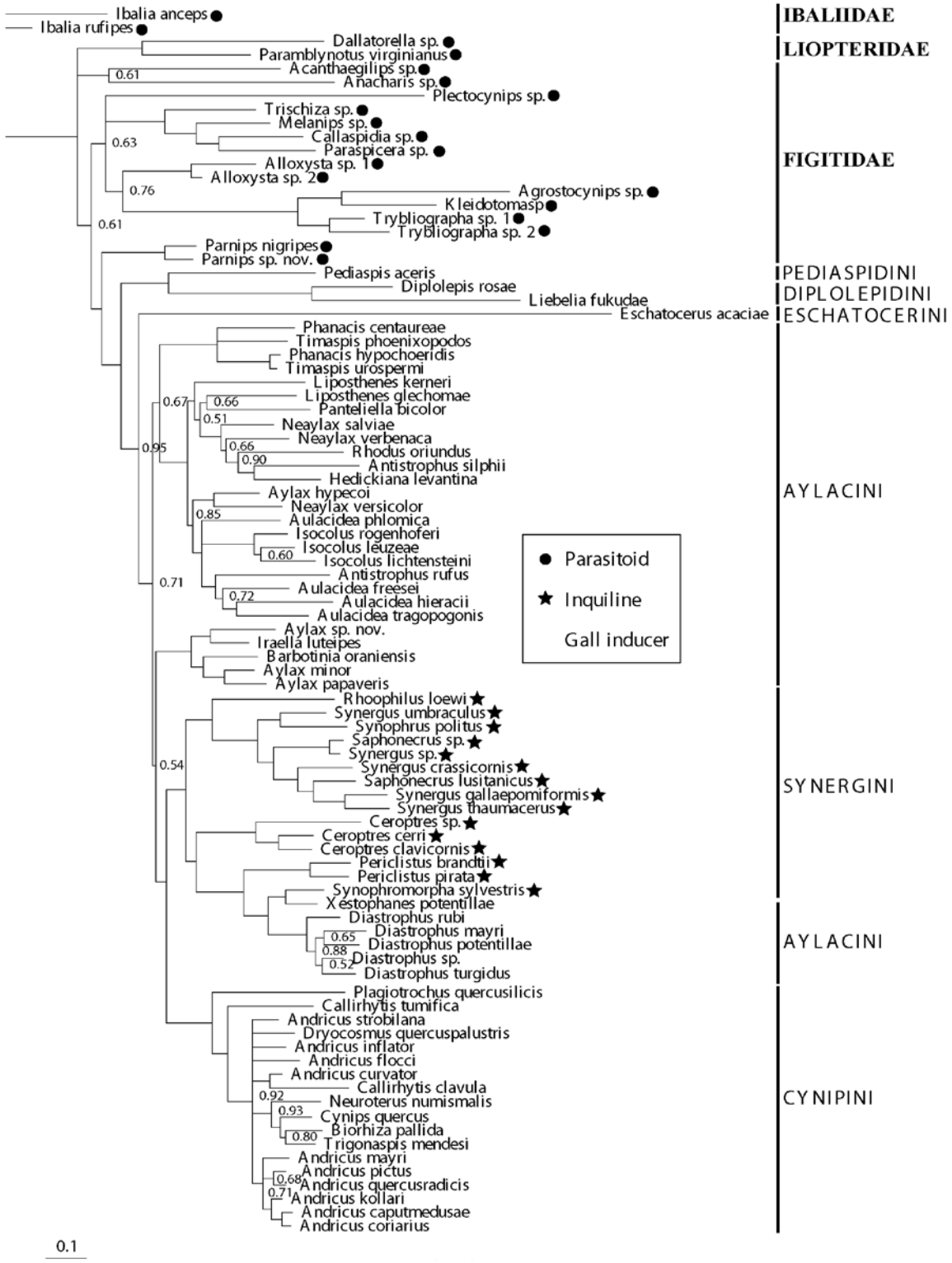

Figura 2. Cladograma mostrando las relaciones filogenéticas de las tribus de la familia Cynipidae. Las tribus Aylacini, Pediaspidini, Diplolepidini, Eschatocerni y Cynipini incluyen las especies inductores de agallas. Las tribus Synergini incluye a las especies inquilinas que habitan dentro de agallas (Tomado de Nylander, 2004a).

El terguito metasomal más grande usualmente es el cuarto abdominal en Figitidae pero ocasionalmente el tercero (Parnipinae; algunos charipinos, anacharitinos y trasorinos). En cinípidos inductores de agallas, el terguito metasomal más grande es el tercero abdominal; en cinípidos inquilinos (Synergini), sin embargo, el más grande es el cuarto abdominal, el cual está típicamente fusionado con el tercero (Buffington & Ronquist, 2006).

La clasificación actual divide la familia Cynipidae en dos subfamilias: Hodiernocynipinae (todos extintos) y Cynipinae (la mayoría de especies vivientes y varias fósiles) (Ronquist, 1999; Liu *et al.,* 2007). Las especies existentes en la familia se encuentran agrupadas en las tribus inductoras de agallas: Aylacini, Eschatocerini, Pediaspidini, Diplolepidini y Cynipini (Nieves-Aldrey *et al*., 2001). Las especies que viven como inquilinos o parasitoides en agallas, principalmente de otros cinípidos, se agrupan en las tribus Synergini y Paraulacini (Nieves-Aldrey, 2001; Liu & Ronquist, 2006; Nieves-Aldrey *et al*., 2009) (Fig. 2). Los Aylacini primariamente se componen de inductores de agallas y no son monofiléticos (Liljeblad & Ronquist, 1998; Ronquist, 1999). Eschatocerini, Pediaspidini, Diplolepidini y Cynipini son monofiléticas, cada una, asociada con plantas hospedadoras leñosas en el linaje rósido de eudicotiledóneas. Los Synergini y los Paraulacini son considerados monofiléticos (Ronquist, 1994, 1999; Liljeblad & Ronquist, 1998; Nieves-Aldrey *et al.,* 2009). Sin embargo, análisis filogenéticos recientes donde se combinan caracteres morfológicos y moleculares indican claramente que los Synergini podrían ser un grupo no monofilético (Nylander *et al*., 2004b; Nylander *et al*., in prep.).

La mayoría de las tribus de cinípidos tienen su centro de distribución en las zonas templadas de la Región Holártica, pero algunas de ellas son endémicas o se extienden dentro de otras regiones zoogeográficas. Sólo cinco géneros son oriundos de las zonas templadas del hemisferio Sur: dos de Suráfrica (*Rhoophilus* y otro que esta en proceso de descripción (Nieves-Aldrey com. pers.) y tres de América del Sur (*Paraulax*, *Eschatocerus* y *Cecinothofagus*) (Pujade-Villar & Hanson, 2006; Nieves-Aldrey *et al*., 2009).

Biología de la familia Cynipidae

Con arreglo a su biología los Cynipidae se dividen en dos grandes grupos: inductores de agallas e inquilinos. El primer grupo esta formado por aquellas especies

que son capaces de inducir la formación de cecidias en plantas; el segundo esta integrado por distintos géneros y especies que no tienen la facultad cecidógena y viven como inquilinos obligados en las agallas producidas por otros cinípidos (Nieves-Aldrey, 2001). Hay que hacer notar, sin embargo, que datos actuales sugieren que las especies incluidas dentro del recién creado género *Cecinothofagus* de la tribu Paraulacini se comportan como parasitoides dentro de agallas inducidas por especies del género *Aditrochus* (Pteromalidae) (Nieves-Aldrey *et al.,* 2009).

Cynipidae inductores de agallas

La inducción de agallas es considerada la más compleja asociación entre insecto y planta en el mundo natural (Shorthouse *et al*., 2005). Los formadores de agallas controlan el desarrollo de los tejidos de su hospedador (Mani, 1964). En consecuencia son fitófagos especialistas relacionados en la mayoría de los casos con una única especie de planta (Raman *et al*., 2005; Shorthouse *et al*., 2005). Las agallas o cecidias pueden ser definidas como "estructuras anormales de partes de los tejidos u órganos de las plantas que se desarrollan por la reacción específica a la presencia o actividad de un organismo inductor". El organismo inductor utiliza la agalla como un medio de procurarse nutrición especializada y cobijo frente al medio ambiente y enemigos naturales. La morfología y complejidad de la agalla es considerada el fenotipo extendido de la especie inductora (Rohfritsch & Shorthouse, 1982; Ananthakrishnan, 1984; Nieves-Aldrey, 1998; Stone *et al.,* 2002; Stone & Schönrogge, 2003; Csóka *et al.,* 2005).

Uno de los rasgos distintivos de los Cynipidae, que los diferencian del resto de las familias incluidas en Cynipoidea, es su asociación obligatoria con diversas familias de plantas, en las cuales inducen la formación de agallas. La tribu Aylacini incluye especies formadoras de agallas en plantas de las familias Asteraceae, Rosaceae, Lamiaceae, Valerianaceae, Papaveraceae, Apiaceae, Brassicaceae y Smilaceaea; las especies de la tribu Eschatocerini forman agallas en *Acacia* y *Prosopis* (Fabaceae); los Pediaspidini inducen agallas en *Acer* (Sapindaceae); los Diplolepidini son gallícolas en plantas del género *Rosa* (Rosaceae) y los Cynipini están asociados particularmente a plantas de la familias Fagaceae, principalmente al género *Quercus* (robles), pero también a los géneros *Castanea*, *Lithocarpus* y *Chrysolepis* (Nieves-Aldrey, 2001; Liu & Ronquist, 2006; Abe *et al.,* 2007). La facultad de inducir la producción de agallas o

cecidias en las plantas no es exclusiva de los cinípidos y ocurre en otros muchos grupos de artrópodos, pero las agallas producidas por los cinípidos son las más especializadas y estructuralmente complejas de todas las zoocecidias. Las agallas de los cinípidos son de tipo histoide prosoplasmaticas, es decir, cecidias que presentan estructuras morfológicas anormales, cualitativamente diferentes a los órganos de las plantas donde se originan, con alto grado de diferenciación tisular dependiendo de la especie de cinípido inductora. La agalla representa una rica fuente de alimento para la larva, a la vez que le proporciona protección frente al ambiente externo y los predadores y parasitoides (Nieves-Aldrey, 2001; Melika, 2006). Las agallas de los cinípidos pueden ser uniloculares las cuales contienen una única cámara larvar y pluriloculares con numerosas cámaras larvales. Las últimas tienen su origen en la puesta cercana o adyacente de múltiples huevos. Las agallas pueden formarse sobre hojas, tallos, yemas y frutos; también en partes subterráneas de la planta como raíces y estolones. La forma de las agallas, especialmente en los Cynipini (especies asociadas a *Quercus*), es muy variada. Pueden ser esféricas, ovales, fusiforme, cilíndricas, lenticulares o bien exhibir otras formas más complejas.

Las agallas inducidas por los Cynipidae constituyen "puntos calientes" ecológicos, ya que proporcionan la base para una multitud de especies animales, principalmente otros insectos (Nieves-Aldrey, 2001; Askew *et al.,* 2006). Las comunidades asociadas a las agallas se estructuran en varios niveles tróficos, formando redes a veces muy complejas integradas por insectos inquilinos, parasitoides y sucesores (Askew, 1984) (Fig. 3). En el tejido de las agallas, además de la larva o larvas del cinípido inductor, viven también las larvas fitófagas de otras especies de cinípidos que no pueden inducir la formación de agallas: los inquilinos, letales o no letales. Dependiendo de estas larvas se estructura otro nivel trófico compuesto de himenópteros parasitoides cuyas larvas viven a expensas de las del cinípido propietario, de los inquilinos y de otros parasitoides, en cuyo último caso son hiperparasitoides (Nieves-Aldrey, 2001). Los parasitoides pertenecen en su mayor parte a la superfamilia Chalcidoidea, aunque también aparecen algunas especies aisladas de Ichneumonidae y Braconidae (Askew, 1984; Nieves-Aldrey, 2001; Hayward & Stone, 2005). La fauna de parasitoides e inquilinos asociadas a agallas de Cynipidae en áreas como el Paleártico occidental ha sido recientemente catalogada (Askew *et al*., 2006) sin embargo, el conocimiento de esta comunidades asociadas a las agallas en el Neotrópico es nulo.

Figura 3. Relaciones bióticas que se dan dentro de una agallas inducida por *Disholcaspis bettyannae* en tallos de *Quecus bumelioides*. Arriba, a la izquierda, el adulto inductor; a la derecha, un corte de la agallas mostrando la cámara del inductor ocupada por una especie de parasitoide del género *Torymus*, alrededor de está las cámaras y las larvas de *Synergus elegans* (inquilino cinípido). Debajo; a la izquierda, el adulto de *Synergus elegans* y a la derecha el adulto de *Ormyrus venustus* otro parasitoide recuperado de la agalla.

Los cinípidos inquilinos

Los cinípidos inquilinos carecen de la facultad que presentan la mayor parte de los cinípidos de inducir agallas y sus larvas fitófagas viven a expensas de las agallas producidas por estos últimos. Esta relación en la que el inquilino es filogenética y taxonomicamente cercano a su hospedador se ha denominado agastoparasitismo (Ronquist, 1994). Aunque sin capacidad cecidógena, a menudo las larvas de los inquilinos tienen el efecto de modificar de algún modo las agallas hospedadoras, bien ensanchándolas, atrofiándolas o deformándolas en mayor o menor medida, estos efectos son dependientes de la etapa de desarrollo de la agalla en la que se produce el ataque, según si éste entraña o no la muerte del cinípido anfitrión (Nieves-Aldrey, 2001). El huevo del inquilino se deposita en el interior de la agalla en crecimiento y la larva

fitófaga se alimenta de los tejidos de aquella. Aunque normalmente se desarrolla sin perjuicio para la larva del cinípido hospedante, hay especies que invariablemente depositan sus huevos cerca de su cámara larval ocasionándole la muerte, bien de forma directa o indirecta al formar sus propias cámaras larvales a expensas de la del propietario original (Nieves-Aldrey, 2001). Estas especies de inquilinos se denominan letales ya que siempre producen la muerte del inductor de la agalla. Las especies inquilinas desempeñan un importante papel en las comunidades asociadas con agallas de cinípidos y afectan en gran medida la supervivencia del cinípido inductor y la complejidad de las comunidades de parasitoides asociadas con distintos tipos de agallas.

Nueve géneros de cinípidos son reconocidos como inquilinos, todos incluidos dentro de la tribu Synergini: *Periclistus* Forster, *Synophromorpha* Ashmead, *Synergus* Hartig, *Saphonecrus* Dalla Torre & Kieffer, *Synophrus* Hartig, *Roophilus* Mayr, *Ceroptres* Hartig, *Ufo* Melika & Pujade-Villar y *Agastoroxenia* Nieves-Aldrey & Medianero. Las relaciones filogenéticas de los géneros presentes en el Paleártico han sido analizadas recientemente por Penzes *et al*., (2009) y Acs *et al.,* (2010). Otros dos géneros: *Paraulax* y *Cecinothofagus,* incluidos dentro de la recién creada tribu Paraulacini, presentan una biología aún incierta, siendo inquilinos o parasitoides en agallas de calcídidos pteromálidos, en lugar de ocupar agallas de otros cinípidos (Nieves-Aldrey *et al.,* 2009).

Ciclo biológico de los Cynipidae

Los Cynipidae presentan tres modalidades de reproducción: bisexual normal, partenogenética telítoca y heterogonia. La primera es semejante a la que presentan la mayoría de los Hymenoptera y la partenogenética telítoca es un tipo de reproducción con desarrollo de hembras diploides a partir de huevos no fertilizados y en la que los machos son muy raros o desconocidos. La mayoría de las especies de Cynipini y Pediaspidini presenta un ciclo de vida con alternancia de dos generaciones distintas (heterogonia): una generación bisexual (hembras y machos) alterna con una generación unisexual (hembras) (al menos en las zonas templadas del hemisferio norte) (Nieves-Aldrey, 2001; Stone *et al.,* 2002; Csóka *et al.,* 2005; Pujade-Villar & Hanson, 2006). Esta característica del ciclo biológico es poco frecuente en los animales; fuera de los Cynipidae (Cynipini y Pediaspidini), se observa en algunos rotíferos, tremátodos, crustáceos cladóceros, Cecidomyiidae (Diptera) y Aphidoidea (Hemiptera) (Stone *et al*.,

2002; Pujade-Villar & Hanson, 2006). En muchos de estos grupos hay varias generaciones asexuadas y una sola generación sexual por ciclo, pero en Cynipidae es común tener una generación bisexual y una unisexual, también denominada ágama, por año las cuales son morfológicamente diferentes en su estado adulto como en la forma y ubicación de la agalla que inducen, por lo que muchas veces se han descrito como especies diferentes (Nieves-Aldrey, 2001; Stone *et al.,* 2002; Csóka *et al.,* 2005; Pujade-Villar & Hanson, 2006). En Europa, unas pocas especies de Cynipini completan su ciclo de vida en dos especies de *Quercus* de distinta sección (heteroecia), una para cada generación, la mayoría de las especies completa su ciclo en una sola especie de planta o en especies de *Quercus* de la misma sección (heterogonia) (Nieves-Aldrey, 2001; Stone *et al.,* 2002). Hasta el momento se desconoce el ciclo de vida completo de casi todas las especies de Cynipidae tropicales y de muchas de Norteamérica (Pujade-Villar & Hanson, 2006).

Los Cynipidae de la región Neotropical y de Panamá

En el Neotrópico, los cinípidos han sido poco estudiados (Díaz *et al*., 2002), a pesar que se piensa que los mayores linajes de avispas inductoras de agallas han divergido en Norte América (principalmente de México donde 160 especies de robles son conocidas) y Centroamérica (Kinsey, 1936). En la actualidad se desconoce el número de géneros y de especies de cinípidos presentes en dicha región (Pujade-Villar & Hanson, 2006). Tres trabajos de reciente publicación ponen de manifiesto la situación actual del conocimiento de la familia Cynipidae en la Región, son estos: "Estado del conocimiento de los Cynipoidea en la Región Neotropical" (Díaz *et al.,* 2002); "Familia Cynipidae (Las avispas cecidógenas)" (Pujade-Villar & Hanson, 2006) y "Familia Cynipidae" (Liu & Ronquist, 2006). Aunque esta información es una excelente ayuda, la misma adolece de nuevos datos de campo y se restringen a una revisión bibliográfica y aspectos generales de la biología de la familia en otras zonas biogeográficas.

La única información de campo generada en la región neotropical proviene de los muestreos realizados por Jorge Champion entre 1879-1883 durante su viaje de colecta por América Central para la obra Biología Centrali-America. Champion realizo colectas generalizadas de insectos durante dos años en Guatemala y dos más en Panamá, incluyendo seis especies de cinípidos que luego fueron reportadas por Cameron (1883). Otro autor que aportó datos de la fauna de cinípidos del Neotrópico

fue Alfred Kinsey, uno de los principales estudiosos de las especies de Cynipidae en Norteamérica, quien en su segundo viaje de colectas de cinípidos llegó hasta Guatemala proveniente de los Estados Unidos. De estas colectas en Guatemala Kinsey describió tres nuevas especie del Neotrópico, a las cuales hay que sumar una especie que previamente se había descrito de la parte de México que se incluye en dicha zona biogeográfica. En los tiempos modernos las principales aportaciones al conocimiento de la fauna de cinípidos neotropicales las encontramos en las realizadas por J. L Nieves-Aldrey, quien ha efectuado prospecciónes en países como; México, Chile, Argentina y Panamá. Como resultado de estas expediciones en en Neotrópico Nieves-Aldrey ha incrementado notablemente el conocimiento de los Cynipidae en dicha región, incluyendo la descripción de numerosas nuevas especies para la ciencia. Sus observaciones realizadas en Panamá son la causa directa que origina esta investigación, ya que solo una especie; *Andricus (Cynips) championi* Cameron 1883, había sido citada en dicho país.

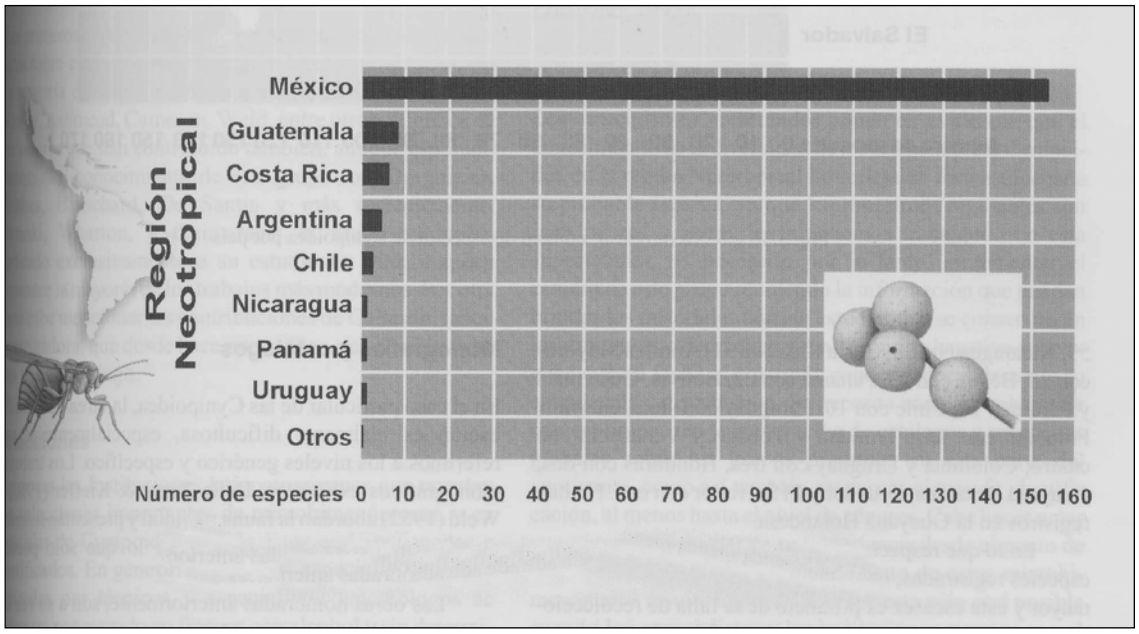

Figura 4. Número actual de especies conocidas de la familia Cynipidae por país dentro de la región Neotropical, según Díaz *et al*. (2002). El número de especies que se reporta para México corresponde a colectas realizadas en la región Neártica, solo *Amphibolips dampfi* Kinsey, es descrita del estado de Oaxaca sur de México área geográfica que pertenece a la región Neotropical.

Otros aportes importantes al conocimiento de la fauna de cinípidos neotropicales la encontramos en Mayr (1881), quien describió el género *Eschatocerus* de Uruguay*;*

Kieffer (1904), quien describió el género *Paraulax* de Chile, Kieffer y Joergensen (1910), quines agregaron dos especies más al género *Eschatocerus* colectados de Argentina. Reciente aportaciones las tenemos en Ritchie & Shorthouse (1987), quienes describieron tres nuevas especies de la tribu Synergini encontradas en la colección Kinsey y que habían sido colectadas en Guatemala por éste; Díaz & Gallardo (1998), quienes describen la primera y única especie de cinípido conocida de Nicaragua y Pujade-Villar quien ha descrito las dos especies de cinípidos conocidas de Costa Rica (Pujade-Villar, 2008; Melika *et al.,* 2009).

En términos generales el conocimiento que se tiene de la familia Cynipidae en la región neotropical es precario, comparado con otras áreas del planeta como Europa (Nieves-Aldrey, 1994, 2001; Rokas *et al*., 2003; Melika, 2006; Nieves-Aldrey *et al*., 2006; Hellrigl, 2008) y Norte América (Burks, 1979; Russo, 2007), donde según Cornell (1985) las especies inductoras de agallas de la tribu Cynipini parecen estar más relacionadas a los robles blancos. Es por ello que en el Neotrópico urge generar conocimiento básico de las especies que se encuentran en esta zona (alfa taxonomía), intentar establecer las relaciones con sus plantas hospederas y los periodos de mayor susceptibilidad de las plantas al ataque de los insectos, identificar las comunidades de otros organismos asociadas a sus agallas e intentar establecer las relaciones filogenéticas de los Cynipidae neotropicales con los de otras regiones mejor conocidas. Como quiera que las especies de cinípidos están obligatoriamente ligadas a sus plantas anfitrionas, los limites de distribución potenciales de sus respectivas áreas de distribución tienden a ser coincidentes, por lo que cabría esperar que en el Neotrópico se encuentren especies de cinípidos asociadas a especies del género *Quercus* (robles) a lo largo de las áreas de distribución de estos árboles, que en el área que nos ocupa coincide con las zonas montanas de América Central, llegando hasta Colombia.

Debido a que en Centroamérica la mayor parte de las especies de *Quercus* se distribuyen en bosques montanos, a elevaciones superiores a 500 metros sobre el nivel de mar y que estas formaciones vegetales están sometidas a una alta presión por las actividades humanas, y el calentamiento global, la realización de inventarios es apremiante para poder generar programas de conservación y manejo de estos bosques tropicales. La conservación de estas áreas montanas amenazadas garantizaría la protección de la riqueza de las especies de Cynipidae y por ende del proceso coevolutivo que representa esta singular relación entre los robles y las avispas de la

familia Cynipidae.

Estructura de esta Tesis

Con arreglo a los objetivos particulares que nos hemos planteado los resultados de esta tesis han sido divididos en tres capítulos constituidos por ocho manuscritos. Siete de los manuscritos estan redactados en idioma inglés, pero al inicio de cada uno de ellos se presenta una resumen en castellano al igual que el estatus de publicación en el que se encuentra el artículo. En todos los casos los manuscritos mantienen el formato de las revistas donde han sido sometidos o publicados.

El primer capítulo esta constituido por un manuscrito no publicado en el que se actualiza el conocimiento de la familia Cynipidae en la región Neotropical; en él se incluyen los resultados generales de esta investigación así como los géneros y las especies descritas dentro de la tesis. En este capítulo se explica de una manera detallada la metodología empleada, de forma tal que la investigación pueda ser reproducida por otros investigadores en cualquier otro sitio, igualmente se incluyen todas las localidades visitadas asi como los periodos de muestreo.

El segundo capítulo se ocupa de las especies inductoras de agallas de la tribu Cynipini. El capítulo esta constituido por cinco manuscritos, en cada uno de los cuales se describen las especies encontradas en Panamá de cinco géneros representativos de la fauna neotropical de Cynipini y que, por su menor diversidad o complejidad taxonómica han permitido culminar con éxito su revisión taxonómica en el área geográfica de estudio. Dichos géneros son los siguientes: *Amphibolips*, *Bassettia*, *Disholcaspis*, *Loxaulus* y *Odontocynips*.

El tercer capítulo aborda las especies inquilinas estudiadas. Este capítulo consta de dos manuscritos en el primero se describe un nuevo género de inquilino y en el segundo se citan de Panamá 10 especies del género *Synergus*, ocho de las cuales son especies nuevas para la ciencia. Igualmente se realiza un análisis filogenético, basado en caracteres morfológicos del adulto y caracteres de biología, de las especies de inquilinos estudiadas.

Completa esta tesis una sección preliminar de morfología y anatomía de las especies de la familia Cynipidae, asi como una discusión general final seguida de las conclusiones que se han derivado de nuestro trabajo.

OBJETIVOS

1. **GENERAL:**

Realizar el primer estudio sistemático de los Cynipidae (Hymenoptera: Cynipoidea) de Panamá: estudiar la taxonomía, faunística, riqueza de especies, biología y relaciones ecológicas de los cinípidos inductores de agalla de Panamá y de su comunidad asociada de cinípidos inquilinos.

2. **PARTICULARES**:

2.1. Actualizar el conocimiento de las tribus, géneros y especies de la familia Cynipidae presentes en la Región Neotropical mediante revisión de literatura y muestreos de campo en la república de Panamá.

2.2. Identificar y describir las nuevas especies de la tribu Cynipini incluidas en los géneros *Amphibolips*, *Disholcaspis*, *Loxaulus*, *Bassettia* y *Odontocynips* colectados en Panamá.

2.3. Revisar taxonómicamente los cinípidos inquilinos de la tribu Synergini de Panamá. Describir nuevas especies y efectuar un estudio filogenético basado en la morfología externa del adulto.

MORFOLOGÍA Y ANATOMÍA DEL ADULTO Y ESTADOS INMADUROS DE LA FAMILIA CYNIPIDAE

Los Cynipidae son insectos de talla pequeña o mediana (1-6 mm), casi siempre alados, aunque existen formas braquípteras y ápteras, con colores sombríos, no metálicos y cuerpo normalmente esculpido. La pubescencia es variable, desde muy escasa en géneros como *Neuroterus* Hartig, a moderada o fuerte, como ocurre en las formas ágamas de especies de *Cynips* Linnaeus. Los cinípidos tienen el cuerpo generalmente ornamentado con diferentes tipos de escultura, cuya forma y disposición suele ser importante para su determinación especifica, rara vez genérica. En general los machos son ligeramente más pequeños que las hembras y, dentro de éstas, las generaciones ágamas (que se reproducen por partenogénesis) suelen tener mayor talla que las de la generación sexual. Por otro lado, en algunos casos, como ocurre en muchas especies de inquilinos del género *Synergus*, aparece una notable variabilidad en la talla corporal (Nieves-Aldrey, 2001).

Los Cynipidae presentan antenas de 12 a 15 artejos, uno más en los machos, con el primer flagelómero por lo común modificado. Placa pronotal generalmente ausente o indistinta, al igual que la carena pronotal latera. La vena cubital del ala anterior (Rs+M) llega, cuando es visible, a un punto más cercano al punto medio de la vena basal que a la confluencia de las M+Cu. Tibias de las patas medias y posteriores con dos espolones. El metasoma de la hembra suele estar comprimido lateralmente; el terguito metasomal más largo es el segundo o bien aparecen el segundo y el tercero fusionados. Hipopigio por lo general prolongado apicalmente en una espina ventral más o menos desarrollada (Nieves-Aldrey, 2001). En la presente tesis se sigue la terminología y abreviaturas morfológicas propuestas por Ronquist & Nordlander (1989), Ronquist (1995), Nieves-Aldrey (2001) y Liljeblad *et al.* (2008).

Medidas y abreviaturas

La medidas absolutas en milímetros, que se dan en las talla de las especies que se describen en esta tesis, se tomaron mediante una escala micrométrica incorporada al estereo-microscopio y se refieren a la talla mínima y máxima medida en las series de ejemplares observados. El resto son todas relativas y fueron las siguientes (Fig. 1 y 2).

Cabeza (Fig. 1 A-C): Anchura de la cabeza en vista dorsal (ancd); longitud de la cabeza en vista dorsal (lcd); anchura de la cabeza en vista frontal (ancf); altura de la cabeza en vista frontal (alcf); línea o distancia ocelar posterior (POL) (distancia entre los márgenes internos de los ocelos posteriores); línea o distancia ocular-ocelar (OOL)

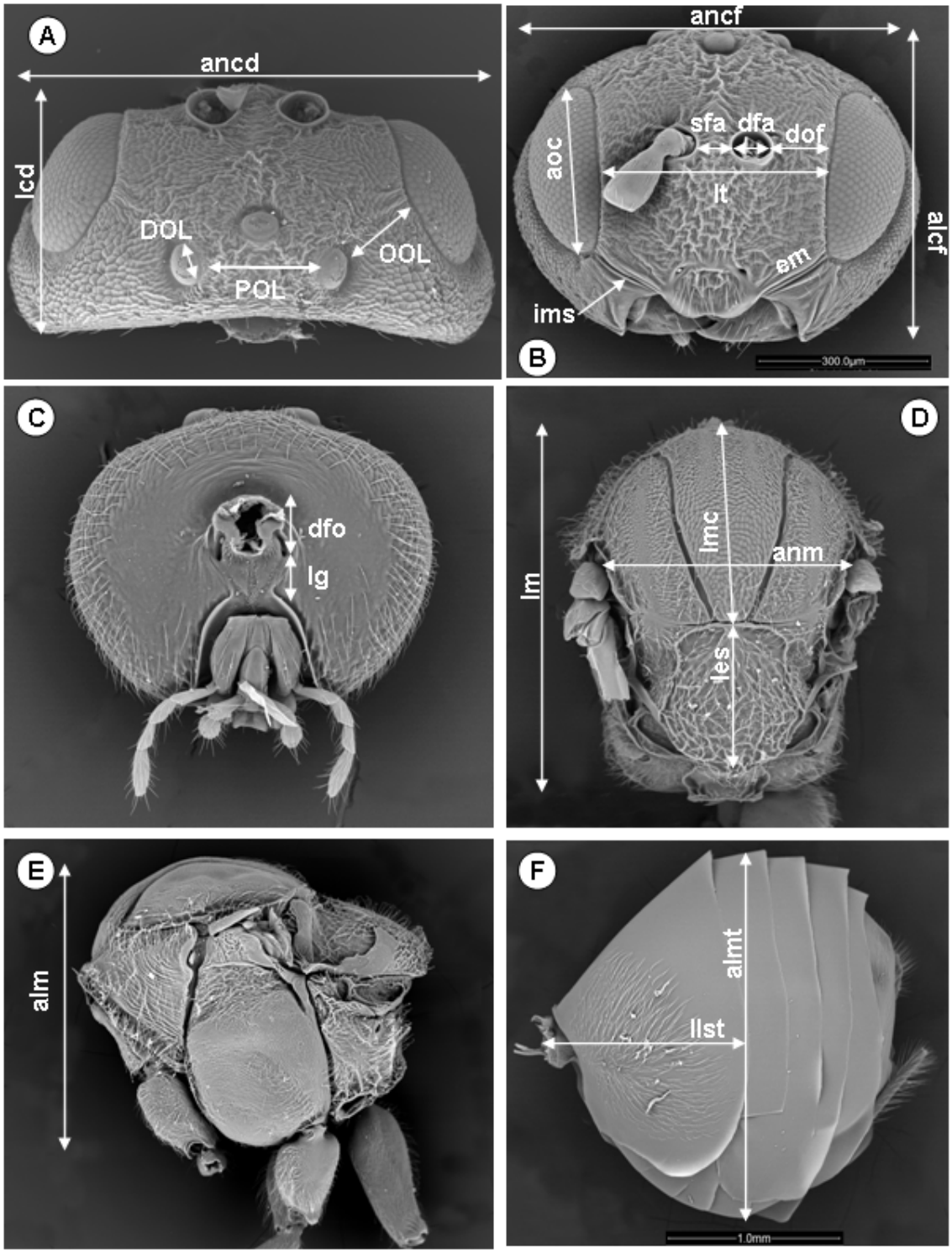

Figura 1. Medidas relativas tomadas en las descripciones morfológicas de los ejemplares de cinípidos. (A) Cabeza en vista dorsal. (B) Cabeza en vista frontal. (C) Cabeza en vista posterior. (D) Mesosoma en vista dorsal. (E) Mesosoma en vista lateral. (F) Metasoma en vista lateral. Explicaciones de las abreviaturas en el texto.

(distancia mínima entre el margen de un ocelo posterior y el margen interno de un ojo compuesto); diámetro de un ocelo lateral (DOL), línea o distancia transfacial o

interocular (lt) (la distancia más corta entre el margen interno de los ojos compuestos, medida a través de las fosetas antenales); espacio malar (em) (distancia entre el margen inferior de un ojo compuesto y la cavidad oral, medida a través del surco o impresión subocular); altura de un ojo compuesto, en visión frontal (aoc); distancia o separación de los márgenes internos de las fosetas antenales (sfa); distancia entre el margen interno de un ojo compuesto y el margen externo de una foseta antenal (dof); diámetro de una foseta antenal (dfa); diámetro del foramen occipital (dfo); longitud gular (lg) (distancia entre el foramen occipital y el oral de la cabeza en visión occipital).

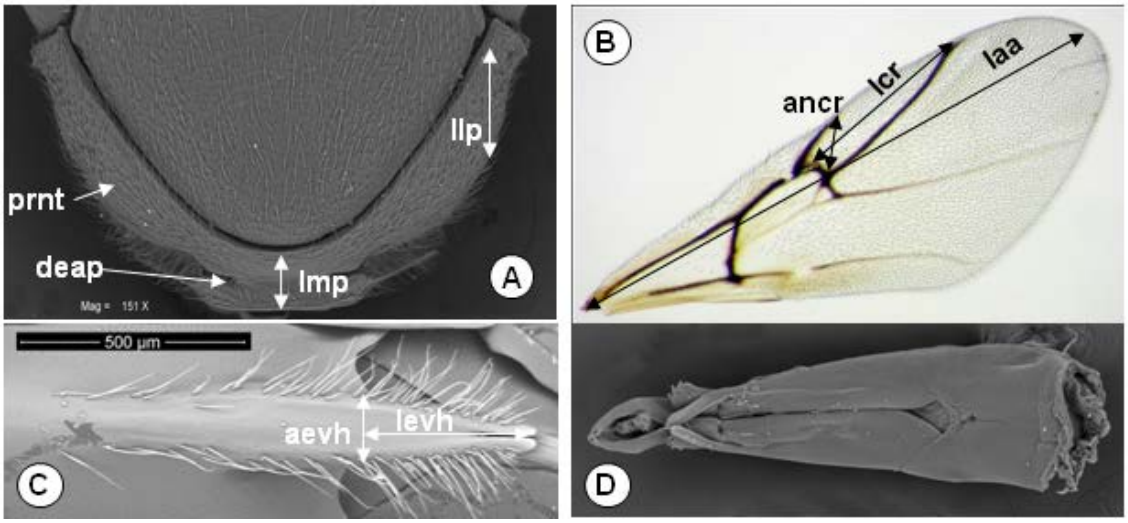

Figura 2. Medidas relativas tomadas en las descripciones morfológicas de los ejemplares de cinípidos, *continuación*. (A) Pronoto, vista dorsal. (B) Ala, vista dorsal. (C) Hipopigio, visión ventral. (D) Genitalia del macho, visión ventral. deap: depresiones admedianas del pronoto, prnt: pronoto.

Mesosoma (Figs.1D-E y 2A): Longitud del mesosoma (lm) (la máxima distancia en visión dorsal entre el extremo anterior del pronoto y el posterior de la nucha del propodeo); anchura del mesosoma (anm) la máxima distancia entre las tégulas en vista dorsal); altura del mesosoma (alm) (la máxima distancia entre el borde superior del mesoescudo y el inferior de la mesopleura); longitud medial del pronoto (lmp) (en vista frontal y medido en la línea media del pronoto, distancia entre los márgenes anteriores del pronoto y mesoescudo); longitud lateral del pronoto (llp) (en visión frontal, la distancia a través del margen lateral del pronoto hasta el punto de confluencia con el margen antero-lateral del mesoescudo); longitud del mesoescudo (lmc) (distancia entre el margen anterior del mesoescudo en visión dorsal y la fisura transescutelar); longitud

del escutelo (les) (distancia entre el extremo inferior de la fisura trasescutelar y el extremo posterior del escutelo en visión dorsal).

Alas (Fig. 2B): Longitud del ala anterior (laa); longitud de la celda radial (lcr) (distancia entre el punto de confluencia de los márgenes internos de las venas R_1 y 2r y el de la vena Rs con el margen alar); anchura de la celda radial (ancr) (distancia entre el punto de confluencia de los márgenes internos de las venas 2r y Rs y el de la vena R_1 y el margen anterior alar).

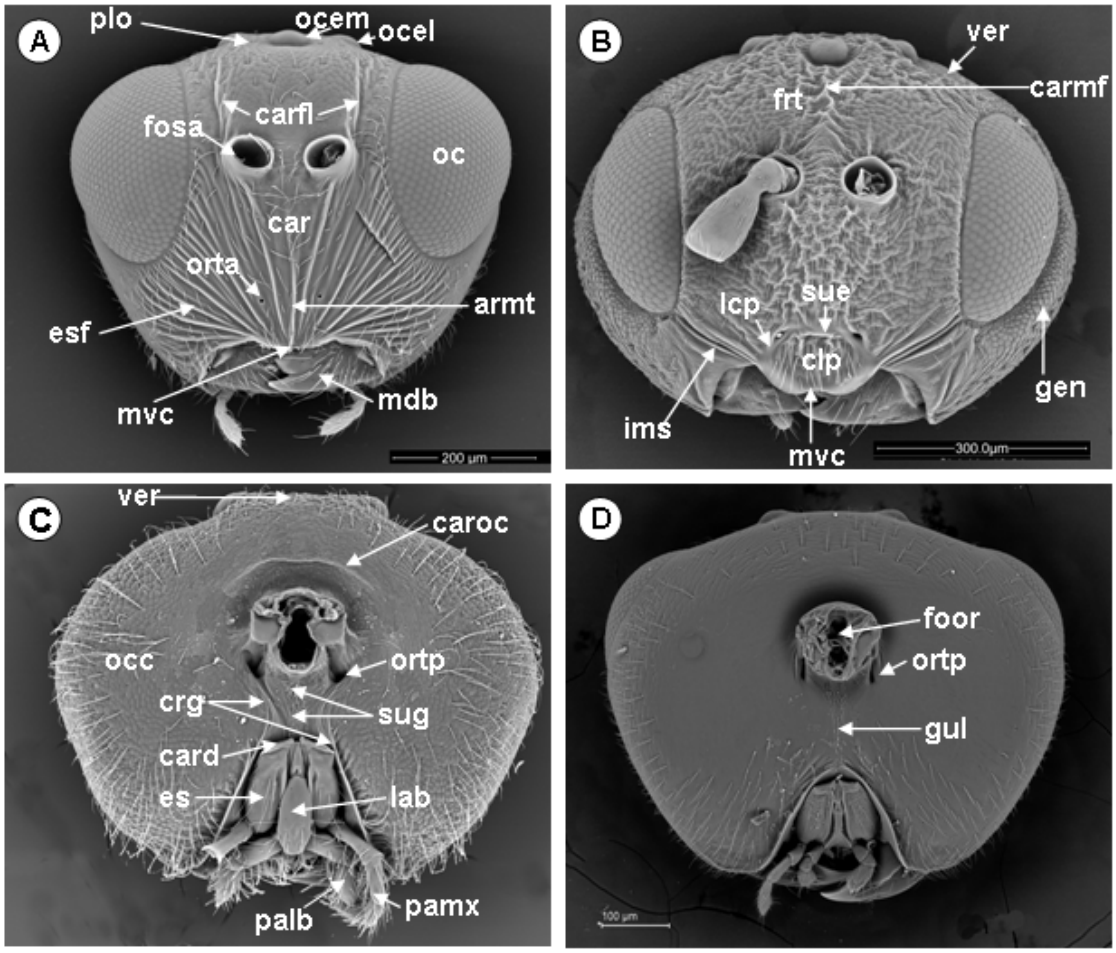

Fig. 3. Caracteres morfológicos de la cabeza de: (A) *Synergus gabrieli* (B) *Callirhytis sp.* (C) *Cynips sp.* (D) *Synergus elegans*. armf: arista media facial, car: cara, card: cardo, carfl: carenas frontales laterales, clip: clípeo, crg, crestas gulares, caroc: carena occipital, carmf: carena media frontal, es: estipe, esf: estrías faciales, foor: fosa oral, fosa: fosetas antenales, frt: frente, gen: gena, gul: gula, hipt: hipostoma, ims: impresión subocular, lab: labio, lcp: líneas clípeo-pleuroestomales, mdb: mandíbulas, mvc: margen ventral del clípeo, oc: ojo compuesto, occ: occipucio, ocel: ocelo lateral, ocem: ocelo medio, orta: orificios tentoriales anteriores, ortp: orificios tentoriales posteriores, palb: palpos labiales, pamx: palpos maxilares, plo: placa ocelar, sue: surco epistomal, sug: surcos gulares, ver: vertex.

Metasoma (Fig. 1F): Longitud del metasoma (lmt) (distancia entre el extremo anterior del peciolo abdominal y el posterior del hipopigio en visión dorsal); anchura del metasoma (anmt) (la máxima distancia transversal entre los tergitos, en visión dorsal); altura del metasoma, en visión lateral, (almt); longitud del segundo tergito metasomal en visión lateral (llst); longitud de la espina ventral del hipopigio (levh); anchura de la espina ventral del hipopigio (aevh) (Fig. 2C).

Cabeza (Fig. 1 A-C y 3). Es hipognata por lo general transversa en vista dorsal (Fig. 1A), mientras que en vista frontal puede ser redondeada o más o menos trapezoide (Fig. 3A-B). Los ojos compuestos son grandes, se hallan situados lateralmente; entre ambos se sitúan, en la parte media dorsal, tres ocelos, uno medio y dos laterales, formando una placa ocelar de forma triangular (Fig. 3A). Las sienes suelen estar dilatadas, a veces de modo acusado, por detrás de los ojos compuestos en las hembras ágamas, mientras que no lo están o parecen poco ensanchadas en las hembras de la generación sexuada. En vista frontal (Fig. 3A-B), entre los ojos compuestos se aprecian las fosetas antenales o toruli (Fig. 3A), donde se insertan las antenas, generalmente situadas en un punto intermedio entre el vértex y el margen inferior del clípeo. Entre el vértex y las fosetas antenales se encuentra la frente, en la frente a veces se observan las escrobas antenales (depresiones que alojan el escapo antenal), que suele estar delimitadas por un par de carenas laterales frontales (Fig. 3A) y a veces también una carena medial frontal (Fig. 3B). El área comprendida entre las fosetas antenales y la cavidad oral se denomina cara, en muchos géneros la cara esta recorrida por estrías o crestas faciales, de longitud variable, que parten en abanico desde el clípeo y pueden llegar hasta la inserción de las antenas (Fig. 3A). En la parte inferior de la cara se encuentran un par de pequeños orificios denominados orificios tentoriales anteriores, que corresponden a la invaginación del esqueleto interno de la cabeza o tentorio y están unidos por una línea o surco epistomal. El surco epistomal y las líneas clípeo-pleurostomales delimitan el clípeo cuyo margen ventral puede ser recto (Fig. 3A) o estar prolongado inferiormente y escotado o no medialmente (Fig 3B). Entre el margen inferior de los ojos compuestos y el clípeo se observa, en algunos géneros de Cynipini, una impresión subocular (Fig. 3B). Si se separa la cabeza del tórax, en vista occipital (Figs. 3C-D), se observa un gran orificio circular, el foramen occipital o foramen magnum y, a ambos lados, un par de pequeños orificios alargados que son los hoyuelos tentoriales posteriores de los que parten un par de crestas gulares (Fig. 3C) que

delimitan un surco medial o surco gular; el surco gular puede ser relativamente largo y las crestas gulares unirse mucho antes de alcanzar el hipostoma (limites de la fosa oral donde se encuentran los apéndices bucales), como ocurre en los géneros de inquilinos (Fig. 3D) o, por el contrario, ser relativamente corto, con la crestas gulares bien separadas o unidas sólo a la altura del hipostoma, como sucede en algunos géneros de *Cynipini* (Fig. 3C). El área que rodea el foramen magnum es el occipucio y a veces se haya separado de la parte superior del vertex por una carina occipital. Las piezas bucales incluyen un par de mandíbulas, maxilas y el labio. Las mandíbulas están bien desarrolladas; son subcuadrangulares y muy esclerotizadas, la derecha normalmente tiene tres dientes y la izquierda dos. El labro es pequeño y se encuentra oculto por el clípeo. Las maxilas estan compuestas de cardo y estipe, con los siguientes apéndices: lacinia, gálea y palpos de cuatro a cinco artejos que surgen del extremo lateral apical del estipe. El labio está compuesto de un postmentón pequeño, débilmente esclerotizado, y un prementón corto membranoso. Los palpos labiales tienen dos o tres segmentos insertos en un foseta situada lateral y apicalmente en el prementón (Fig. 3C).

Las antenas de los cinípidos son filiformes o ligeramente ensanchadas hacia el ápice. Está compuesta de un artejo basal o escapo, un pequeño artejo intermedio, corto y globoso, el pedicelo, y un flagelo terminal integrado por 10 a 15 artejos (Fig. 4A). El primer flagelómero antenal suele estar modificado en los machos, aparece excavado y curvado en el medio y más o menos ensanchado en el ápice (Fig. 4C-D), y el flagelo antenal tiene, por lo general, un artejo más que la antena de la hembra. Los artejos del flagelo llevan sedas normales y también un tipo especial de sedas sensoriales denominadas sensilas placoideas (Fig. 4B).

Mesosoma (Fig. 2A y 5). Es el segundo tagma corporal y comprende el tórax y el primer segmento abdominal fusionado con él, denominado propodeo. El pronoto o placa dorsal del protórax alcanza por detrás las tégulas, donde se insertan las alas; es corto y adopta forma de U en visión frontal (Fig. 2A). En las tribus *Aylacini* y *Synergini* es relativamente largo en la parte media y suele presentar un par de depresiones admedianas separadas, asociadas o no a una placa pronotal, con márgenes laterales más o menos marcados. En los *Diplolepidini* y *Cynipini*, el pronoto es medialmente muy corto y las depresiones admedianas son indistintas, a veces unidas por un surco longitudinal superficial. La superficie lateral del pronoto puede presentar en el género *Synergus* una carena lateral.

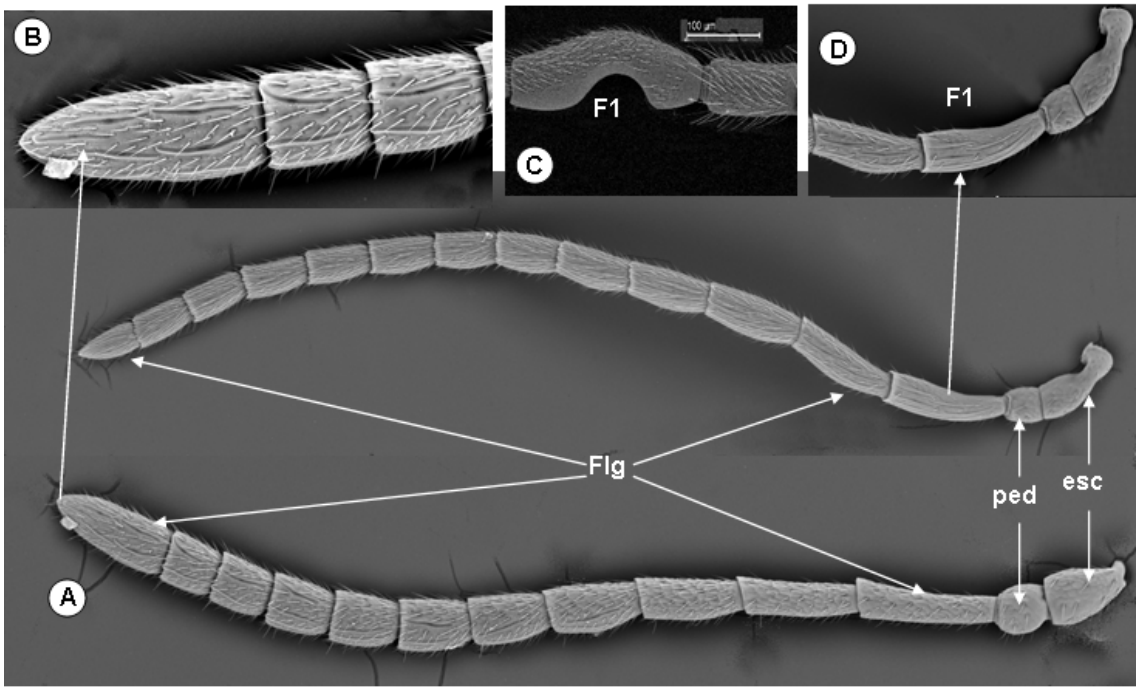

Figura. 4. Antenas de Cynipidae. (A) Antena de la hembra y macho de una especie del género *Callirhytis*. (B) Ampliación de los tres últimos segmentos de la antena de la hembra mostrando las sensilas placoideas. (C-D) Modificación del primer segmento del flagelómero de la antena de machos en Cynipidae. (C) Macho de *Agastoroxenia panamensis* (*Synergini*). (D) Macho de una especie del género *Callirhytis* (*Cynipini*), esc: escapo, flg: flagelo, F1: primer flagelómero.

El mesonoto o placa dorsal del mesotórax está compuesto por un esclerito anterior, el mesoescudo, y otro posterior el escutelo (Fig. 5A). El mesoescudo es dorsalmente convexo y por lo general esculpido y se halla recorrido por una serie de líneas o surcos; los notaulos (Fig. 5A) son dos impresiones o surcos, convergentes posteriormente en la fisura transescutelar, y pueden ser completos, con márgenes bien definidos en todo su recorrido, más o menos difuminados o indistintos en el tercio o mitad anterior del mesoescudo o bien casi enteramente ausentes. Entre los notaulos, en la parte posterior del mesoescudo, se encuentra una impresión o surco mesoescutal mediana que se extiende anteriormente de forma variable y no supera por lo general la mitad del mesoescudo. Lateralmente, el mesoescudo lleva dos surcos o signa parapsidales y en la parte anterior dorsal dos surcos o signa anteromedianos. El mesoescudo esta normalmente separado del escutelo por una fisura o surco transescutelar, a veces obsoleta o ausente. Posteriormente a la fisura transescutelar se encuentran un par de fosetas escutelares que suelen estar separadas por un tabique o

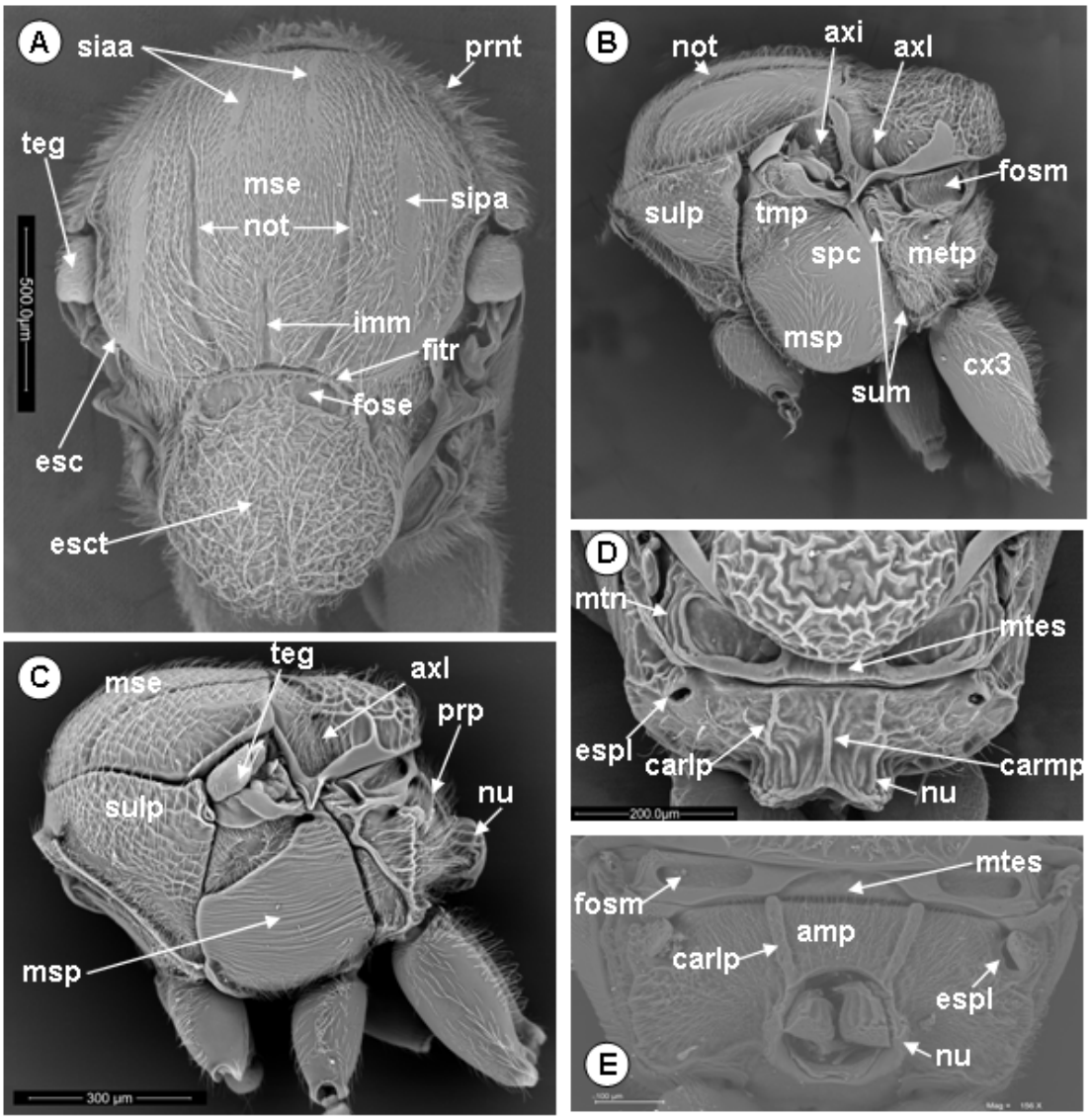

Figura 5. Caracteres morfológicos del mesosoma de cinípidos. (A) *Disholcaspis* (B) *Cynips*. (C & E) *Synergus*. (D) *Callirhytis*. amp: área media del propodeo, axi: axila, axl: axilula, carlp: carenas laterales del propodeo, carlpr: carena lateral del pronto, carmp: carena media del propodeo, deap: depresiones admedianas del pronoto, esc: escudo, esct: escutelo, espc: especulo, espl: espiráculos, fitr: fisura transescutelar, fose: fosetas escutelares, fosm: fosetas metanotales, imm: impresiones mesoescutal mediana, metp: metapleura, mse: mesoescudo, msp: mesopleura, mtes: metaescutelo, mtn: metanoto, not: notaulos, nu: nucha, plpr: placa pronotal, prnt: pronoto, siaa: signa anteromedianos, sipa: signa parapsidales, sulp: superficie lateral del pronoto, sum: surco metapleural, teg: tégulas, tmp: triángulo pleura.

septo pero que, en ocasiones, pueden ser confluentes e indistintas formando una ligera depresión transversa. La profundidad de las fosetas escutelares es variable, así como su forma y tamaño, lo que proporciona caracteres discriminantes en la separación de especies. El escutelo es un esclerito de forma oval o redondeada y superficie dorsal

plana o más a menudo convexa. La superficie antero-lateral del escutelo recibe el nombre de axila (Fig. 5B-C); anteriormente, en los flancos del escutelo, se encuentran dos depresiones denominadas axilulas, más o menos superficiales, y cuyo margen posterior dorsal puede estar o no marcado. Las mesopleuras (Fig. 5 B-C) están constituidas por un triángulo mesopleural situado en la región anterior dorsal, una zona media oblicua más o menos esculpida y un área postero-lateral, normalmente sin escultura denominado espéculo. Las esculturas de la mesopleura tienen importante valor taxonómico en la diagnosis genérica y específica.

El metanoto (Figs. 5B-E) corresponde a la placa dorsal del tercer segmento torácico o metatórax; en los cinípidos es muy reducido y lo compone dos fosetas o depresiones metanotales alargadas, separadas por una zona más elevada central denominada metaescutelo o dorsellum que puede presentar una constricción mediana más o menos acentuada. Las metapleuras (Fig. 5B) presentan en el margen anterior lateral un surco metapleural cuyo extremo anterior puede situarse en una situación más o menos elevada sobre el margen postero-lateral de la mesopleura. El propodeo (Fig. 5C-E) es el primer segmento abdominal que se ha fusionado al tórax en los Hymenoptera Apocrita; en él se aprecian dos carenas laterales paralelas, arqueadas o anguladas, las cuales limitan el área media propodeal, cuya forma tiene importante carácter diagnóstico en los géneros de *Cynipini*. En géneros como *Plagiotrochus*, *Loxaulus*, *Bassettia* y algunas especies de *Callirhytis* se aprecia también una carena media, completa o no, situada entre las dos carenas laterales (Fig. 5D). En los lados del propodeo se encuentra un par de espiráculos relacionados con el aparato respiratorio traqueal. La parte media posterior del propodeo es estrecha, en forma de un anillo más o menos alargado, se denomina nucha y se articula con el primer segmento del metasoma o peciolo (Figs. 5D-E).

Las alas (Figs. 6E-F) están por lo general presentes, aunque pueden aparecer más o menos reducidas o faltar completamente. El número de alas es el típico de dos pares, el anterior mucho más grande que el posterior. Las alas anteriores y posteriores se anclan por una serie de ganchos denominados hamuli. Las anteriores son largas, generalmente hialinas y pubescentes. El margen distal alar puede llevar o no sedas más o menos largas (fimbria marginal). La venación típica de un cinípido, siguiendo la terminología estándar para himenópteros de Manson (1986) se muestra en la figura 6E. La venación es muy reducida, presenta una característica celda radial más o menos

triangular o trapezoidal alargada (celda marginal para algunos autores) que puede estar completamente cerrada en el margen alar por la prolongación de la primera rama de la vena radial (R1) o más o menos abierta en el ápice, la base y/o el margen, cuando las dos ramas de la vena radial (R1 y Rs) no alcanzan el margen anterior del ala. Debajo de la parte anterior de la celda radial puede ser o no visible otra pequeña celda triangular denominada areola (ar). Carácter distintivo de la familia es que la vena cubital (Rs+M), cuando es visible encuentra la vena basal en un punto más cercano a la parte media de dicha vena que al punto de confluencia de la basal con la medial más la cubital 1(M+Cu). Sin embargo, en algunos *Aylacini* la cubital casi llega a dicho punto de encuentro al igual que sucede en la familia Figitidae.

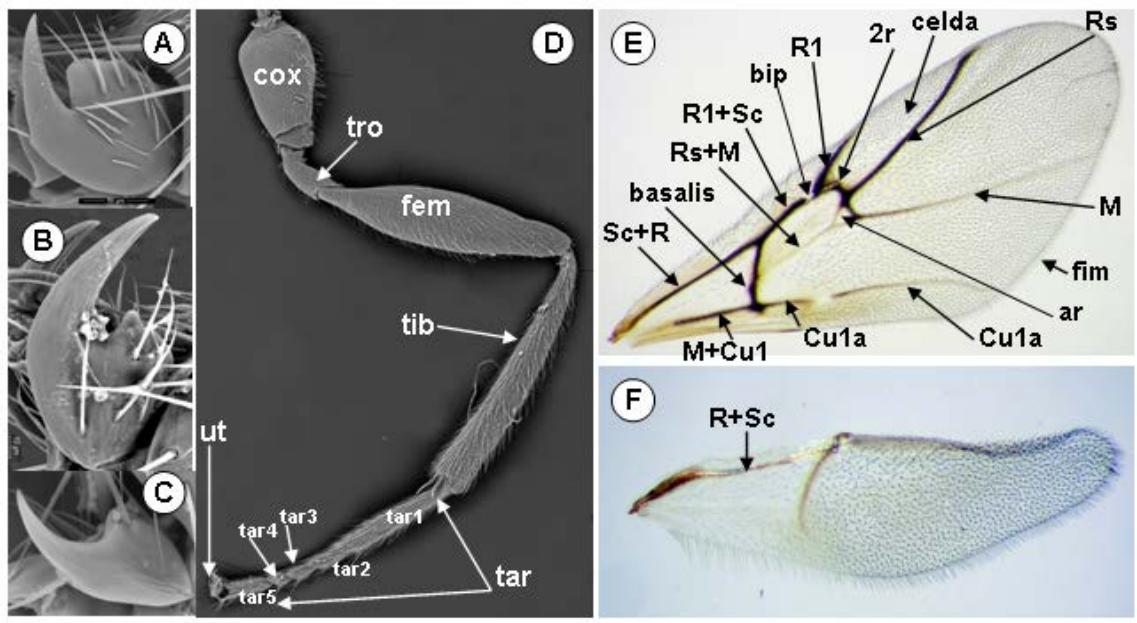

Figura 6. Caracteres morfológicos de las patas y alas de Cynipidae. (A-C) uña metatarsal mostrando diferentes formas del diente o lóbulo basal. (D) pata posterior. (E) Ala anterior (F) ala posterior. cox: coxa, fem: fémur, tar: tarso, tib: tibia, trocánter, ut: uña tarsal. Cu: vena cubital, fim: fimbria marginal, M: vena medial, R: vena radial, Sc: vena subcosta.

La areola puede estar o no presente. Las alas posteriores son mucho más pequeñas y estrechas que las anteriores; por lo común el borde inferior alar posee sedas relativamente más largas. La venación alar está muy reducida y sólo son visibles tres venas: subcostal mas radial (Sc+R), medial más cubital 1(M+Cu) y Media (M).

Hay tres pares de patas (Figs. 6A-D) correspondientes a cada uno de los segmentos torácicos. Se componen de coxa, trocánter, fémur, tibia, y tarsos (Fig. 6D).

Los fémures no están engrosados y carecen de espinas o dientes. Las tibias de las patas anteriores llevan un espolón largo y curvado asociado a unos peines de sedas, situados en el primer tarsómero, que utilizan en la limpieza de las antenas, las tibias de las patas medias y posteriores están provistas apicalmente de un par de espolones desiguales. Los tarsos tienen cinco artejos, el primero más largo que los restantes. El último tarsómero lleva dos uñas que pueden ser simples (Fig. 6C) o bien presentar un lóbulo basal o diente más o menos pronunciado, de modo que las uñas parecen bifidas (Fig. 6A-B).

Metasoma (Fig. 7) Es el tercer tagma corporal visible y constituye el abdomen aparente. El metasoma de los cinípidos muestra una compresión lateral característica. El abdomen en la hembra consta de siete segmentos visibles. Los terguitos son grandes y se extienden ventralmente, cubriendo las extensiones dorsales de los esternitos. El segundo tergito abdominal (primero metasomal) suele estar muy reducido, en ocasiones, como sucede en el género *Synergus*, se halla más desarrollado, tiene forma de anillo acanalado y constituye un pequeño peciolo metasomal.

El tercer terguito abdominal (segundo metasomal) normalmente es grande y cubre gran parte del metasoma; en los géneros de los inquilinos, el tercer terguito se funciona con el cuarto formando un sinterguito, el cual cubre casi la totalidad del metasoma (Fig. 7B). A veces, la fusión es incompleta y el tercer y cuarto terguitos están separados por una sutura obsoleta. Los terguitos pueden ser glabros o más o menos pubescentes. El tercer terguito abdominal puede llevar lateralmente en su base un conjunto o placa de sedas más o menos denso y/o conspicuo, cuya presencia o ausencia reviste importancia taxonómica (Fig. 7B). Los terguitos suelen ser lisos, pero frecuentemente llevan un fino punteado más o menos conspicuo, especialmente en la parte posterior de los últimos terguitos abdominales metasomales. El último esternito visible (séptimo) constituye el hipopigio o placa subgenital; apicalmente está prolongado por una "espina ventral" por la cual se exerta el taladro (tenebra) del ovipositor. La forma, longitud relativa y longitud y disposición de las sedas que presenta la espina ventral son muy variables y constituyen caracteres de importancia taxonómica en los cinípidos (Fig. 7C-E).

El ovipositor en las hembras de Cynipidae es una estructura delgada, de muy pequeño diámetro para minimizar los daños al hospedador. Como mecanismo protector la estructura está invaginada en el abdomen y se han desarrollado métodos

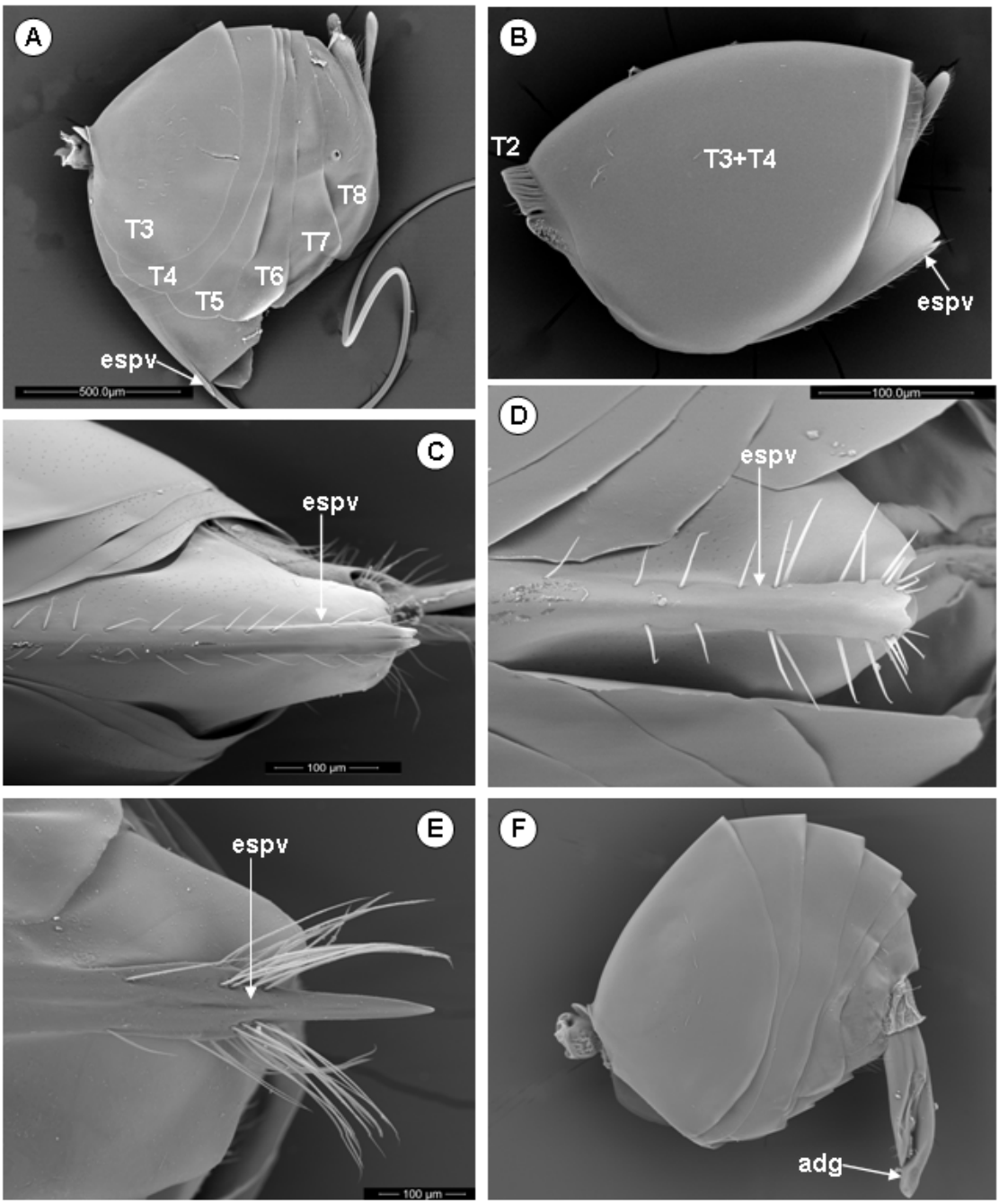

Figura 7. Caracteres morfológicos del metasoma de Cynipidae. (A) Vista lateral de una hembra del género *Callirhytis*. (B-C) Vista lateral y ventral de la hembra de *Synergus gabrieli.* (D) Vista ventral de la espina de una especie de *Dryocosmus*. (E) Vista ventral de la espina de la especie de un nuevo género (F) Vista lateral del macho de una especie de *Callirhytis*. adg: aedeago, esp: espina ventral o hipopigial, T1: terguito abdominal 1.

de invaginación-evaginación. El noveno terguito está profundamente hendido, hasta el punto de que aparece un par extra de estuches del ovipositor. El décimo terguito se fusiona con el noveno y el octavo teguito aparece siempre esclerotizado. El noveno gonocoxito es alargado y casi vertical; representa el principal elemento del sistema de

puesta de los cinípidos y está expandido y curvado hacia arriba en forma de cuerno. El ovipositor tenebra sensu Ronquist y Nordlander (1989), es un tubo que se compone de tres partes: un par de valvas dorsales fusionadas, un par de valvas ventrales surcadas longitudinalmente para recibir las crestas o aristas complementarias de las valvas dorsales, y un par de estuches más anchos que las restantes valvas que encierran. El ápice del ovipositor lleva poros, sedas y estructuras sensoriales que probablemente se usan con el fin de determinar la idoneidad del sustrato para la oviposición.

El sistema genital masculino (Fig. 2D, 5F). Los terguitos noveno y décimo están fusionados en un sinterguito muy reducido; la estructura genital se encuentra protegida ventralmente por el octavo esternito, de pequeño tamaño, denominado placa subgentital. El falo u órgano copulador masculino se compone de un anillo basal esclerotizado que envuelve lateralmente la parte basal de un par de placas paramerales que están prolongadas por unos parámeros y separados dorsal-mente por una línea media. En vista ventral se aprecia que internamente desde los parámeros se proyecta las volselas, cuyo ápice está modificado en un par de digitus bien desarrollados, con su margen dorsal provisto de una hilera de espinas. Entre estos pares de piezas se sitúa centralmente el órgano intromitente denominado pene o aedeago (Fig. 5F). En los cinípidos el aedeago puede o no estar ensanchando de forma característica en la parte subapical; la longitud relativa de los parameros y la forma del digitus proporcionan caracteres que son utilizados en la taxonomía del grupo.

Características de las fases no adultas

El estudio de las formas no adultas como fuente de información para ayudar a entender las relaciones evolutivas de los cinípidos y sus grupos hermanos ha tenido gran interes en los ultimos años. Los principales aportes al incremento del conocimiento de las características de las formas no adultas las encontramos en los trabajos de Vårdal *et al.*, (2003); Vårdal, 2004; Nieves-Aldrey *et al.,* (2005).

Los huevos

Los huevos de los cinípidos son de color blanco o amarillento, de corion liso y pedunculado. Consta de un cuerpo central de forma oval alargada, subcilíndrica o subesférica y un cuello o pedúnculo más o menos alargado, que en su punto de unión con el cuerpo central prolonga su eje longitudinal y está ligeramente ensanchado en su

extremo libre (Nieves-Aldrey, 2001; Vårdal, 2004). La longitud de la parte estrecha o pedúnculo de los huevos es muy variable pudiendo ser en algunas ocasiones varias veces el largo del cuerpo del huevo. Se ha sugerido diferentes funciones para el pedúnculo de los huevos de los cinípidos, algunos autores sugieren que la longitud del pedúnculo del huevo esta estrechamente relacionado con la profundidad a la que los huevos son colocados dentro de los tejidos de su plantas hospedantes, sin embargo dicha longitud en una misma hembra puede ser muy variable (Melika, 2006). Tambien se ha atribuido funciones respiratorias al pedúnculo. Estudios realizados con *Diplolepis* y *Biorhiza* sugieren que la principal funcion del pedúnculo en los huevos de cinípidos es probablemente ayudar al paso de los huevos a través del muy estrecho ovipositor (Nieves-Aldrey, 2001; Vårdal, 2004; Melika, 2006 y referencias allí citadas).

La superficie del huevo es lisa y aparentemente desprovista de regiones especializadas como aeropilas o apéndices respiratorios como se encuentran en los huevos de los Diptera, Hemiptera o Ephemeroptera. El micropilo no forma una estructura fácil de ser detectada como en los huevos otros órdenes de insectos. La cáscara de los huevos de cinípidos esta constituida por dos principales capas, el vitelino en el interior que esta adyacente al oocito y externamente el corion que a su vez esta dividida en el endocorion y el exocorion. El número de huevos que llevan las hembras suele ser elevado pudiendo llegar hasta 1000 en las especies inductoras de agallas en rosa. El elevado número de huevos que llevan las hembras de las especies de los cinípidos sugiere que estas podrian ser pro-ovigenicas, es decir que las hembras emergen con todos los huevos maduros (Vårdal, 2004).

Las larvas

Las larvas de los cinípidos, principalmente las estructuras relacionadas a la cabeza, muestran variaciones en los caracteres los cuales pueden ser potencialmete informativos acerca de las relaciones filogenéticas de los cinípidos (Nieves-Aldrey *et al.,* 2005).

La larva de los cinípidos es eucéfala (Fig. 8A-B), corta, gruesa y carnosa, curvada sobre sí misma en forma de U para acomodarse a la cavidad larval de la agallas (Fig. 9), de color blanquecino y de tegumento liso y glabro con algunas setas concentradas en la cabeza (Nieves-Aldrey *et al.,* 2005). En el cuerpo se distinguen 12 o 13 segmentos; en los segmentos segundo al décimo se localiza un par de espiráculos poco visibles (Fig.

9B). La larva es ápoda y ciega. El tamaño de las larvas varia entre especies pudiendo alcanzar algunas especies de *Andricu*s hasta 7 mm de largo (Melika, 2006).

En los Cynipini las larvas pueden ser de dos tipos, el primer tipo es fusiforme mientras que las del segundo tipo tienen ensanchada la región torácica. Este último tipo de larva puede ser dividido a su vez en dos subtipos, las que tienen los segmentos 1 a 3 del cuerpo dorsalmente protuberantes y las que tienen estos segmentos anchos. La cabeza de los Cynipini suele ser romboide o con una ligera incisión dorsal. El área de las antenas es siempre amplia y conspicua. El labro es ligeramente más estrecho en la base que en el ápice. El margen apical del labro puede ser recto, ligeramente cóncavo o fuertemente hendido. Las mandíbulas pueden ser desde delgadas y completamente expuestas hasta cubiertas completamente por el labro. Las maxilas son generalmente redondeadas. El labio en la mayoría de las especies es redondeado o cuadrado. El número de dientes en la mandíbula varia entre 1 a 5 dependiendo de las especies y es frecuente encontrar asimetría en las madibulas de una misma especie. Se pueden observar setas en el área lateral de la antena, en la gena, en el clíipeo y frecuentemente una seta a cada lado del labio. Pocas especies presentan setas en el labro. Los palpos maxilares y labiales son conspicuos en unas pocas especies pero están probablemente presentes en todas las especies (Nieves-Aldrey *et al.,* 2005)

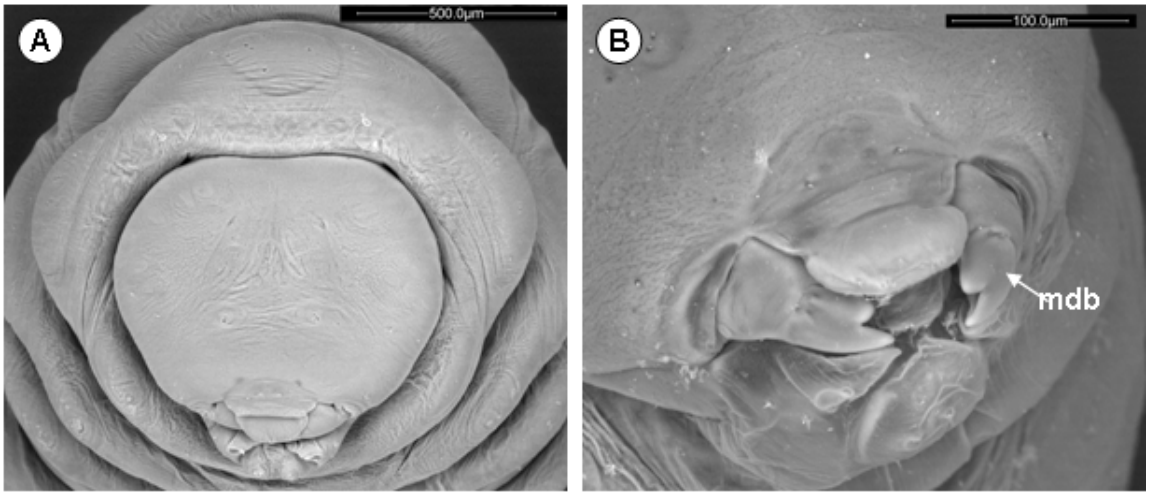

Figura. 8. Vista anterior de la cabeza de dos larvas de cinípido. (A) *Disholcaspis bisethiae,* inductor, mostrando la forma y tamaño de la cabeza con relación al primer segmento. (B) *Synergus gabrieli*, inquilino, mostrando los dos dientes en la mandíbula

La pupa

Cuando la larva está plenamente desarrollada pasa por estado de prepupa antes de producirse la transformación a pupa. El estado de prepupa está relacionado a menudo con el periodo de diapausa para pasar condiciones adversas. Las larvas se alimentan en el interior de la agalla pero, con objeto de evitar la contaminación de la cámara larval, no defeca hasta poco antes de la pupación, denominándose esta excreción meconiun. La pupa es exarata y se asemeja al adulto no completamente formado. La pupación tiene lugar siempre en el interior de la agalla y el adulto emerge abriéndose camino con las mandíbulas a través de ésta.

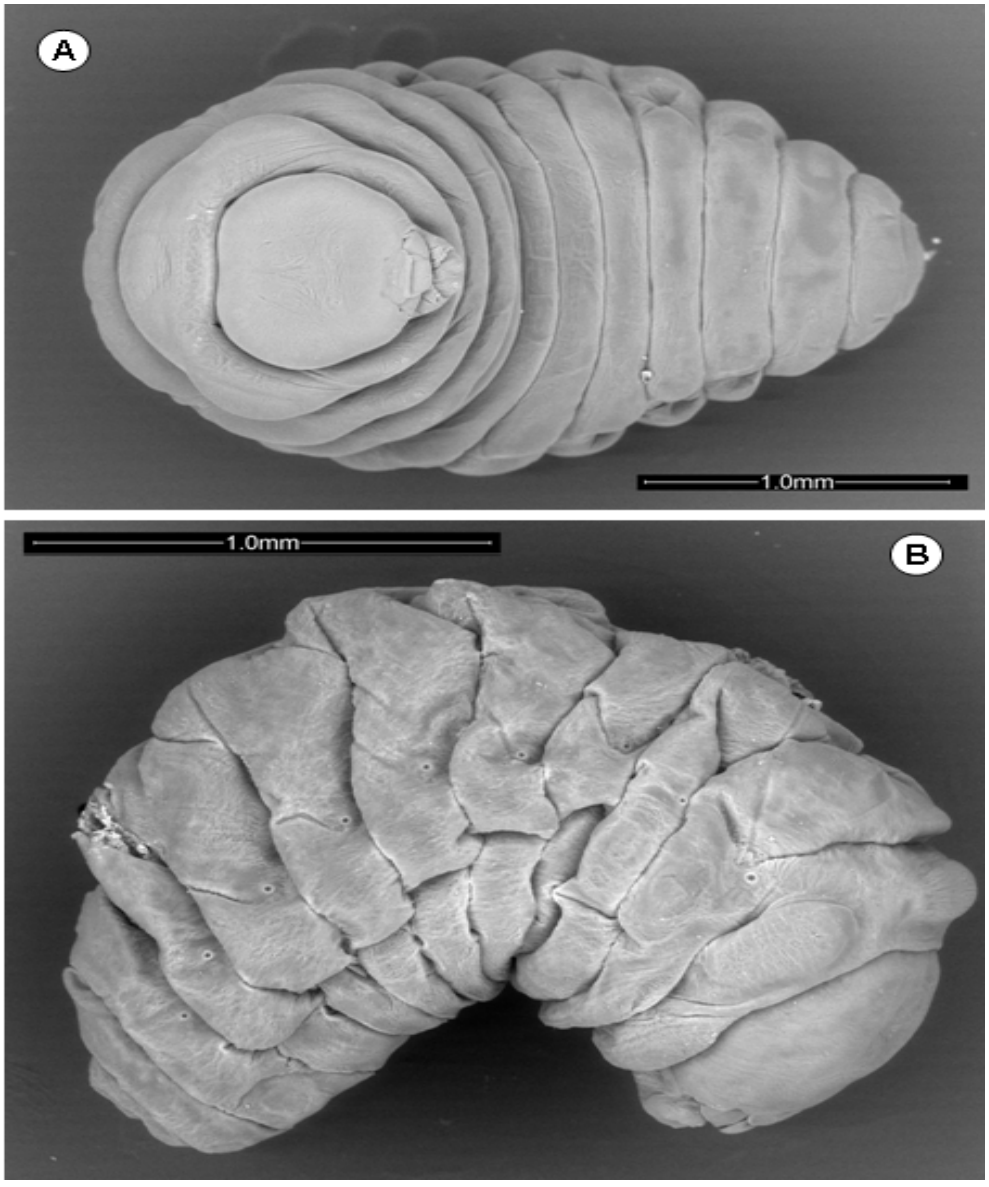

Figura. 9. Larva de ultimo estadio de *Disholcaspis bisethiae* (A) visión ventral. (B) visón lateral.

RESULTADOS

CAPÍTULO 1

Los cinípidos (Hymenoptera, Cynipoidea, Cynipidae) de Panamá

OBJETIVO 1

Actualizar el conocimiento de las tribus, géneros y especies de la familia Cynipidae presentes en la Región Neotropical mediante revisión de literatura y muestreos de campo en la república de Panamá.

1.1- Primer estudio de las avispas de las agallas de la república de Panamá, incluyendo una lista actualizada de los cinípidos neotropicales (Hymenoptera, Cynipidae)[1]

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Resumen

Se ha efectuado el primer estudio faunístico y taxonómico de los cinípidos de Panamá a la vez que se actualiza el conocimiento de las tribus, géneros y especies de esta familia de himenópteros en la región neotropical. Los resultados apoyan la hipótesis de que las montañas de Centroamérica albergan una rica fauna de inductores e inquilinos de las tribus Cynipini y Synergini (Cynipidae). Como resultado de 20 meses de muestreo en los bosques de *Quercus* de las montañas de Panamá se colectaron 65 diferentes agallas inducidas por cinípidos, se obtuvo el adulto inductor de 45 de ellas los cuales se clasificaron en 10 géneros de la tribu Cynipini. Se estima que un 94% de las especies corresponden a especies aún no descritas. Los géneros de cinípidos inductores identificados son: *Andricus* Hartig, con 12 especies; *Neuroterus* Hartig, con nueve; *Dryocosmus* Giraud, con siete especies; *Cynips* Linnaeus, con 4 especies; *Amphibolips* Reinhard, con tres especies; *Disholcaspis* Dalla Torre & Kieffer, *Loxaulus* Mayr y *Odontocynips* Kieffer con dos especies cada género; *Callirhytis* Forster y *Bassettia* Ashmead, con una especie cada uno. Se han identificado 11 especies de inquilinos de la tribu Synergini, 10 del género *Synergus* Hartig, de las cuales 8 son nuevas para la ciencia, y una especie perteneciente al nuevo género *Agastoroxenia*. Adicionalmente dos nuevos géneros de cinípidos inductores, aún en periodo de estudio, han sido

[1] Manuscrito sometido a publicación como; Primer estudio de las avispas de las agallas de la república de Panamá, incluyendo una lista actualizada de los cinípidos neotropicales (Hymenoptera, Cynipidae). Boletín de la Sociedad Entomológica Aragonesa.

detectados en el material colectado. La fauna actual en el Neotrópico de la familia Cynipidae queda actualizada en seis tribus, 18 géneros y 45 especies, 41 de las cuales son nativas y cuatro han sido introducidas en la región. Para Panamá se aporta una lista de 21 especies de la familia Cynipidae, de las cuales 10 son inductores de agallas y 11 son inquilinas. Por último se discute el estado actual de conocimiento de las especies de la familia Cynipidae en la república de Panamá.
Palabras clave**:** Agallas, inductor, inquilino, Cynipini, Synergini, Chiriquí, Panamá

First study of the oak gall wasps of Panama with an updated check list of the Cynipidae of the neotropical region

Abstract: A comprehensive faunistic and taxonomic study of the oak gall wasps of Panama has been made for the first time, and an updated check list of the Cynipidae of the Neotropical Region is provided. The results support the hypothesis than the mountains of Central America host a rich fauna of inducer and inquilines of the Cynipini and Synergini tribes (Cynipidae). Resulting of twenty months of samplings in montane Quercus forest of Panama, sixty five different galls induced by cynipids were collected, the adults inducers of 45 of them were reared and these were classified into 10 genera of the tribe Cynipini. It is estimate that 94% species are undescribed. The genera of cynipids identified are *Andricus* Hartig, 12 species; *Neuroterus* Hartig, 9 species; *Dryocosmus* Giraud, 7 species; *Cynips* Linnaeus, 4 species; *Amphibolips* Reinhard 3 species; *Disholcaspis* Dalla Torre & Kieffer, *Loxaulus* Mayr and *Odontocynips* Kieffer with 2 species each; *Callirhytis* Forster and *Bassettia* Ashmead, with one species each. Eleven species of the tribe Synergini have been identified, 10 species of the genus *Synergus* Hartig, of which 8 are new species and one new genus *Agastoroxenia* with *A. panamensis* are described. In addition two new genera of gall inducers have been detected in the material collected. The current fauna of the family Cynipidae in the Neotropical Region is updated to six tribes, 18 genera and 45 species, 41 of which are native and four have been introduced in the region. For Panama it is provided a list of 21 species of the family Cynipidae, of which 10 are gall inducers and 11 inquilines. Finally the current state of the knowledge of the species in the family Cynipidae at the Republic of Panama is discussed.
Key words: Galls, inducer, inquiline, Cynipini, Synergini, Chiriquí, Panamá

Introducción

Las especies incluidas dentro de la familia Cynipidae constituyen un grupo de insectos singular dentro de la superfamilia Cynipoidea del orden Hymenoptera (Nieves-Aldrey, 2001), las cerca de 1.400 especies descritas, son fitófagas especializadas que inducen agallas o viven como inquilinas dentro de éstas (Csóka *et al.,* 2005; Liu & Ronquist, 2006; Pujade-Villar & Hanson, 2006; Liljeblad *et al*., 2008). Las especies existentes de la familia se encuentran agrupadas en las tribus inductoras de agallas: Aylacini (21 géneros y 170 especies); Eschatocerini (un género y tres especies), Pediaspidini (dos géneros y dos especies); Diplolepidini (dos géneros y 55 especies) y Cynipini (25 géneros y *ca.*1000 especies) (Liljeblad *et al*., 2008). Una tribu recientemente descrita se ha añadido a esta lista, Qwaqwaini Liljeblad, Nieves-Aldrey y Melika, con una especie afrotropical que induce agallas en *Scolopia mundii* (Salicaceae) (Liljeblad *et al.,* 2011). Las especies que viven como inquilinos o parasitoides en agallas, principalmente de otros cinípidos, se agrupan en las tribus Synergini (ocho géneros y 170 especies) y Paraulacini (dos géneros y seis especies) (Nieves-Aldrey, 2001; Liu & Ronquist, 2006; Nieves-Aldrey *et al*., 2009).

Los Cynipidae se encuentran en todos los continentes, con excepción de Australia, que no tiene fauna nativa, aunque unas pocas especies han sido introducidas allí por el hombre (Nieves-Aldrey, 2001). La distribución de la familia es, sin embargo, desigual y la gran mayoría de las tribus de cinípidos están distribuidas en zonas templadas del hemisferio norte dentro de la región zoogeográfica holártica pero, algunas son endémicas o se extienden en otras regiones zoogeográficas (Nieves-Aldrey, 2001). Los Aylacini están representados principalmente en Europa, pero unos pocos linajes importantes están centrados en Norteamérica, la tribu incluye formadores de agallas en plantas de las familias Asteraceae, Rosaceae, Lamiaceae, Valerianaceae, Papaveraceae, Apiaceae, Brassicaceae y Smilaceaea; las especies de la tribu Eschatocerini son endémicas de Suramérica y forman agallas en *Acacia* y *Prosopis* (Fabaceae); los Pediaspidini se distribuyen en el Paleártico occidental e inducen agallas en *Acer* (Sapindaceae); los Diplolepidini están mayoritariamente representados en la región Holártica formando agallas en *Rosa* (Rosaceae) (Nieves-Aldrey, 2001; Liu & Ronquist, 2006). Los Paraulacini viven como parasitoides o inquilinos letales en agallas inducidas por especies del género *Aditrochus* Rübsaamen (Pteromalidae) sobre *Nothofagus* (Fagaceae) en Argentina y Chile (Nieves-Aldrey *et al*., 2009). Los Cynipini y la mayor

parte de los inquilinos de la tribu Synergini, que en conjunto constituyen más del 80% de todas las especies de cinípidos conocidos, presentan una mayor distribución en la región Holártica y están asociados particularmente a plantas de la familias Fagaceae principalmente al género *Quercus* (Nieves-Aldrey, 2001; Liu & Ronquist, 2006). Unas cuantas especies de Cynipini utilizan plantas hospedadoras de otros géneros cercanamente relacionados dentro de las Fagaceae como; *Castanea*, *Castanopsis* y *Lithocarpus* (Stone *et al.,* 2002). La tribu Cynipini ha sido considerada generalmente como un grupo natural y varios estudios filogenéticos basados en caracteres morfológicos y moleculares soportan esta hipótesis (Kinsey, 1920; Ronquist, 1994; Liljeblad & Ronquist, 1998; Nylander, 2004; Liu *et al.,* 2007; Liljeblad *et al.,* 2008). Cada especie de Cynipini esta generalmente asociada a una o un grupo relacionado de especies de *Quercus* induciendo agallas en los órganos de su planta hospedante (Weld, 1952; Ronquist, 1994; Liljeblad & Ronquist, 1998; Nieves-Aldrey, 2001; Stone *et al*., 2002; Csóka *et al.,* 2005). Esta asociación entre las especies de Cynipidae y su planta hospedante determina el patrón de distribución mundial de esta familia de insectos (Nieves-Aldrey, 2001), por lo que en América central y del sur, donde el grupo ha sido poco estudiado y existen muy pocas citas de cinípidos, cabe esperar que las especies inductoras de agallas de la tribu Cynipini y sus inquilinos de la tribu Synergini ocurran donde quiera que las especies de *Quercus* sean abundantes, es decir, a través de las zonas montañosas de Centroamérica y Colombia (Stone *et al*., 2002; Csóka *et al.,* 2005; Nieves-Aldrey, 2005; Liu & Ronquist, 2006).

Los reportes de especies de la familia Cynipidae en el Neotrópico, como hemos mencionado, son escasos (Díaz *et al*., 2002; Liu & Ronquist, 2006; Pujade-Villar & Hanson, 2006), a pesar que hay autores como Kinsey (1936) que estimaban que los mayores linajes de avispas inductoras de agallas habrían divergido en México y América Central. En México y Guatemala, especialmente en las áreas de México norte y central incluidas en la región Neártica se han citado 157 especies de Cynipidae, en su mayoría Cynipini y unas pocas especies de Synergini asociados a *Quercus*, (Kinsey, 1936, 1937a, 1937b, 1938; Pujade-Villar *et al.,* 2009). Hasta este momento se han citado 11 géneros de la familia Cynipidae en el Neotrópico, mientras que cuatro especies de los géneros; *Phanacis* Forster, *Timaspis* Mayr (Aylacini); *Pediaspis* Tischbein (Pediaspidini) y *Plagiotrochus* Mayr (Cynpini) han sido introducidas en la región (Weld, 1926; Pujade-Villar & Díaz, 2001; Nieves-Aldrey & Grez, 2007). Los

géneros de Cynipidae citados en el Neotrópico son: *Eschatocerus* Mayr (Eschatocerini); *Amphibolips* Reinhard, *Andricus* Hartig, *Callirhytis* Foerster, *Disholcaspis* Dalla Torre & Kieffer, *Dryocosmus* Giraud, *Neuroterus* Hartig, *Odontocynips* Kieffer (Cynipini); *Synergus* Hartig (Synergini); *Paraulax* Kieffer y *Cecinothofagus* Nieves-Aldrey & Liljeblad (Paraulacini) (Pujade-Villar & Hanson, 2006; Nieves-Aldrey *et al*., 2009). Sin embargo, hasta el inicio de este trabajo no existía ninguna especie formalmente descrita de los géneros *Amphibolips*, *Callirhytis*, *Disholcaspis, Dryocosmus* y *Neuroterus* y no había registros de la tribu Diplolepidini y sus inquilinos en Centro y Sur de América (Liu & Ronquist, 2006), datos que se han modificado recientemente con la descripción de tres nuevas especies del género *Amphibolips*, dos del género *Disholcaspis*, dos del género *Loxaulus* y una del género *Bassetia* de Panamá (Medianero & Nieves-Aldrey, 2010a, 2010b, 2011; Medianero *et al.*, 2011).

A pesar que en los últimos años se han descrito nuevas especies de Cynipidae de la región neotropical (ver Ritchie & Shorthouse, 1987*;* Díaz & Gallardo, 1998; Nieves-Aldrey, 2005; Pujade-Villar, 2008; Melika *et al*., 2009; Nieves-Aldrey *et al*., 2009; Nieves-Aldrey & Medianero, 2010, 2011; Medianero & Nieves-Aldrey, 2010a, 2010b, 2011 en prensa), en términos generales el conocimiento que se tiene de la familia Cynipidae en la región sigue siendo muy precario comparado con otras áreas como Europa y Norte América (Burks, 1979; Díaz *et al.,* 2002; Nieves-Aldrey, 2001; Melika, 2006). Por ejemplo, en Panamá, que puede ser considerado el límite de distribución del género *Quercus*, (ya que solo *Q. humboldtii* ha sido citada de Colombia), se han identificado nueve especies de estas plantas (Correa *et al.*, 2004), pero solo una especie de Cynipidae había sido citada para este país (*Andricus championi* Cameron, 1883) en el comienzo de este estudio. En Costa Rica existen un número similar de especies de *Quercus* y solo han sido descritas dos especies de cinípidos (*Odontoynips hansoni* Pujade-Villar y *Andricus costaricensis* Pujade-Villar & Melika) aunque existen más de 30 especies de Cynipini colectadas por describir (Pujade-Villar & Hanson, 2006). Por consiguiente y dado que: 1/-el Sur de Norteamérica es considerado uno de los principales centros de diversificación de especies de Cynipidae (Kinsey 1936, 1937b), gracias al elevado número de especies de *Quercus* que se encuentran en esta región; 2/-que un número representativo de estas especies de plantas llegan hasta Panamá y 3/-que existe un al alto grado de especificidad entre las especies de Cynipidae y sus plantas anfitrionas (dependencia que determina los patrones de distribución de estos insectos),

era de esperar la existencia de una rica fauna de cinípidos inductores de agallas e inquilinos en este país. La riqueza de especies debería ser a *priori* al menos similar a la de otras áreas con igual número de especies de *Quercus* registrados, como por ejemplo la Península Ibérica donde cerca de 68 especies, incluidas en 7 géneros de Cynipini han sido identificadas asociadas a 10 especies de *Quercus* (Nieves-Aldrey, 2001), o en Florida (Estados Unidos) donde 88 especies han sido registradas sobre seis especies de *Quercus* (Abrahamson *et al*., 2003; Price *et al*., 2004).

El presente estudio tiene como objetivo recopilar el conocimiento actual de la familia Cynipidae en el Neotrópico y aportar nuevos datos de los géneros de Cynipidae para la región, procedentes de los muestreos realizados en Panamá en los últimos años. Este estudio es el primero en toda Centroamérica en el que se ha planteado un muestreo sistemático y en profundidad de la familia Cynipidae y sus relaciones bióticas. Los únicos estudios de este tipo documentados en el área, referentes a la familia Cynipidae, datan de colectas realizadas por George Champion entre 1879-1883 para la obra Biología-Centrali America y por Alfred Kinsey en 1935-1936, quien es su segundo viaje de colecta de agallas de cinípidos desde Norteamérica llegó hasta Guatemala.

Materiales y Método

Selección de los puntos de muestreo

Las colectas de las agallas inducidas por las especies de cinípidos se realizaron en 19 localidades de muestreo de cuatro provincias de la República de Panamá (8° 58´ N, 79° 32´ O), con presencia registrada de árboles del género *Quercus* (Tabla I). Se efectuaron 20 muestreos mensuales, en 15 de los sitios ubicados en la Cordillera Central del país, una prolongación de la Cordillera del Talamanca que nace en el sur de Costa Rica, entre diciembre de 2007 y agosto de 2010 (Fig. 1). Estos 15 puntos de muestreo que se visitaron con mayor frecuencia, fueron seleccionados por albergar el mayor número de especies y las mayores poblaciones de *Quercus* en Panamá.

Método de muestreo

Para las colectas de las agallas se realizaron muestreos intensivos de duración variable entre cuatro y seis horas por sitio. Con la ayuda de tijeras y una vara podadora de cuatro metros y medio de extensión, se cortaban ramas de las partes aéreas de las plantas y se realizaba una exhaustiva búsqueda de las agallas de cinípidos. Las colectas de las cecidias (agallas) correspondían a diferentes fases de desarrollo aunque preferiblemente

maduras, poco antes de que se produjeran las primeras emergencias de insectos. En un cuaderno de campo y en etiquetas se anotaron todos los datos relevantes asociados a las muestras colectadas (fecha, localidad, altitud e información biológica). Las agallas eran fotografiadas "in situ" con una cámara digital (Canon G9), y guardadas en bolsas de papel o plástico dependiendo de la época del año (lluviosa o seca). Las colectas diarias eran individualizadas en frascos para evitar mezclar más de una agalla, rotuladas y almacenadas hasta su posterior traslado a los laboratorios del Programa de Maestría en Entomología de la Universidad de Panamá. En todos los casos donde se encontró agallas de cada planta hospedadora se tomó una muestra para la identificación de la especie de *Quercus*, para la cual se utilizaron las claves de Burger (1977), D'Arcy (1987), Breedlove (2001). Como ayuda en la identificación se realizaron también comparaciones con material depositado en los herbarios de la Universidad de Panamá y del Instituto Smithsonian de Investigaciones Tropicales (STRI).

En el laboratorio las cecidias se colocaron en cajas de emergencia y las mismas se revisaban cada dos días por un periodo de seis meses hasta que ocurriera la emergencia de los adultos; inductor, inquilino o parasitoides. Una vez transcurrido este plazo de tiempo el material era recogido y almacenado definitivamente en las colecciones del Programa de Entomología de la Universidad de Panamá. En los casos en que el número de agallas colectadas lo permitía, una muestra de ellas era diseccionada para colecta y preservación de estados inmaduros, fundamentalmente las larvas del inductor y los demás pobladores de la agallas (inquilinos, parasitoides y sucesores). Una proporción de los adultos obtenidos de las agallas fue preservada en alcohol al 96%, para disección y estudios moleculares, mientras que el grueso de la muestra fue montada en seco mediante la técnica usual de montaje de microhimenópteros, pegados los insectos de costado en pequeñas etiquetas rectangulares, sobre alfileres entomológicos, para su estudio taxonómico y obtención de una colección de referencia. Colecciones de referencia del material estudiado de adultos montados en seco, adultos y estados inmaduros congelados en alcohol, y de agallas conservadas en seco, se encuentran depositadas tanto en el Programa Centroamericano de Maestría en Entomología de la Universidad de Panamá (MEUP) como en el Museo Nacional de Ciencias Naturales en Madrid (MNCN).

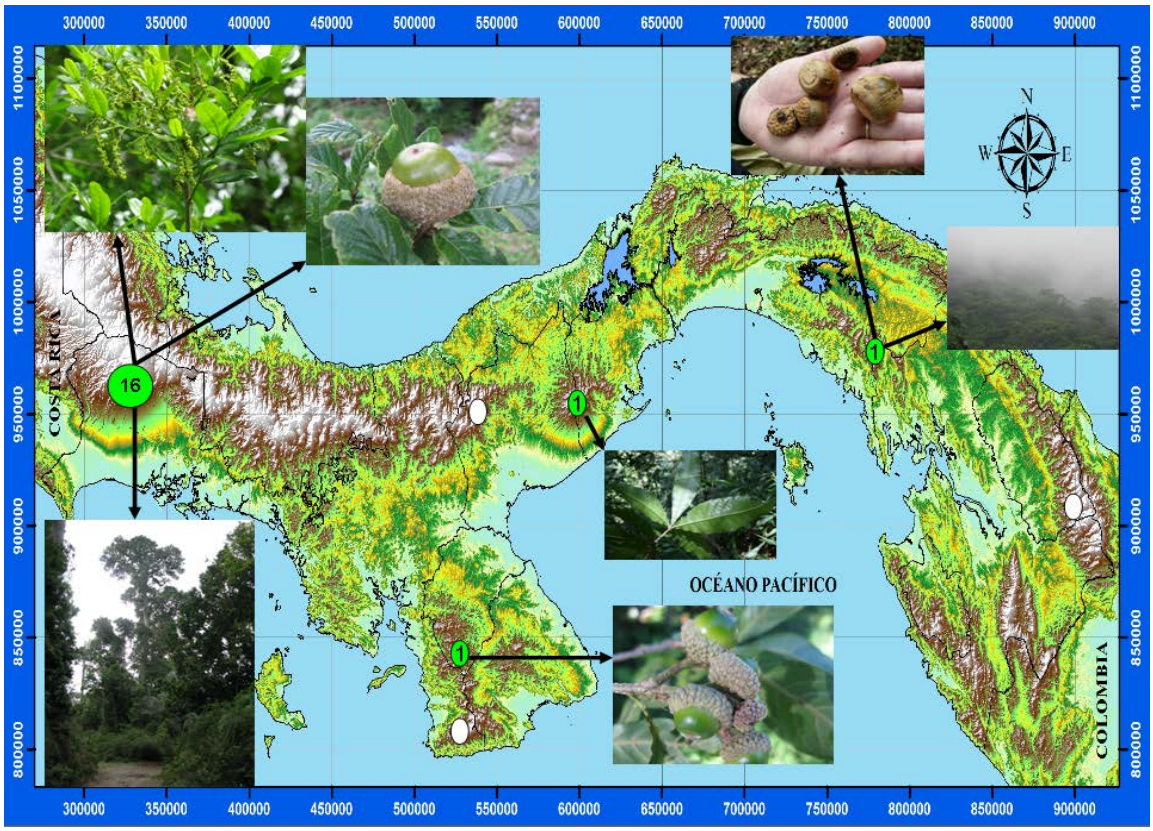

Figura 1. Mapa de Panamá indicando con círculos los sitios donde se han registrado poblaciones del género *Quercus*. Los círculos en verde indican los sitios muestreados en este estudio. El número dentro del círculo indica el número de localidades de muestreo. Las principales poblaciones de *Quercus* en Panamá se encuentran al occidente del país cerca de la frontera con Costa Rica a unos a 450 Km de la ciudad de Panamá.

Preparación de los ejemplares para el estudio taxonómico

El material emergido de las agallas; inductores, inquilinos cinípidos y parasitoides se fotografió con una cámara digital Nikon Coolpix 4500 adaptada a un estéreo microscopio Wild MZ8. Para el análisis sistemático de los caracteres morfológicos los adultos de la familia Cynipidae fueron diseccionados de acuerdo al protocolo establecido por Ronquist y Nordlander (1989), véase también Fontal-Cazalla *et al.,* (2002) y Liljeblad *et al.,* (2008), para su observación mediante microscopía electrónica de barrido (SEM) (aproximadamente 20 fotos por ejemplar, correspondientes a las vistas estandarizadas de las partes morfológicas diseccionadas). Para ello se utilizó un microscopio electrónico modelo EVO 40 VP Zeiss del Instituto Smithsonian de Investigaciones Tropicales (STRI) en Panamá y un FEI QUANTA 200 del Museo Nacional de Ciencias Naturales en Madrid. Para las fotografías con el microscopio electrónico se utilizo, dependiendo del número de ejemplares disponible para disección,

la técnica de alto vacío con material diseccionado (revestido con oro u oro-paladium, 60%/40%), o la técnica de bajo vacío con ejemplares enteros (sin diseccionar ni metalizar). Se realizaron fotografías digitales del ala anterior de los especimenes que habían sido previamente montados en portaobjetos en medio de Euparal.

Identificación taxonómica

Las identificaciones a nivel de género se realizaron con los trabajos clásicos de Dalla Torre & Kieffer, (1910), Houard, (1933), Weld (1952) y los trabajos más recientes de Nieves-Aldrey (2001), Melika & Abrahamson (2002) y Liljeblad *et al*. (2008). En todos los casos se consultaron también las descripciones originales.

Cálculos estadísticos

Se calcularon los estimadores no parametricos Jacknife 1, Jacknife 2 y Bootstrap para estimar la riqueza de especies en el área de estudio. Los cálculos se realizaron con el programa *EstimateS* 8.2 ® (Colwell, 2009).

Resultados

Un total de 1. 436 individuos de la familia Cynipidae fueron colectados en los 20 meses de muestreo en Panamá, de los cuales 770 individuos corresponden a cinípidos inductores de la tribu Cynipini y 667 a inquilinos de la tribu Synergini.

Tribu Cynipini

Se identificaron 65 morfotipos diferentes de agallas inducidas por especies de la tribu Cynipini (Figs 2-5). Se obtuvo el adulto inductor de 45 de ellas (69%), que se clasificaron dentro de 10 géneros (Tabla III). Los individuos emergidos de dos agallas colectadas sobre las hojas y tallos de *Q. bumelioides*, *Q. lancifolia* y *Q. insignis* (secc. Quercus, robles blancos) no pudieron ser incluidos dentro de alguno de los géneros conocidos de Cynipini y se ha determinado como nuevos géneros (Nieves-Aldrey *et al.* en preparación). *Andricus* Hartig con 12, *Neuroterus* Hartig, con nueve y *Dryocosmus* Giraud con siete especies son los géneros de la tribu Cynipini mejor representados en los sitios de colecta (Tabla III). Son de destacar los siguientes resultados taxonómicos. El género *Amphibolips* Reinhard se cita por primera vez en Panamá describiéndose tres nuevas especies para la ciencia (Medianero & Nieves-Aldrey, 2010a; capítulo 2.1 de

esta memoria).

El género *Disholcaspis* Dalla Torre & Kieffer se cita por primera vez en la región neotropical, a la vez que se describen dos especies nuevas de Panama (Medianero y Nieves-Aldrey, 2011; capítulo 2.3 de esta memoria).

Los géneros *Bassettia* Ashmead, y *Loxaulus* Mayr son citados por primera vez para la región Neotropical, a la vez que se describen una nueva especie de *Bassetia* y dos del género *Loxaulus* (Capítulos 2.2 y 2.4 de esta memoria; Medianero y Nieves-Aldrey, 2010b: Medianero *et al*., 2011).

Se ha colectado la agalla y se obtuvo y se ha descrito por primera vez el adulto inductor de la única especie citada hasta el comienzo de este estudio en Panamá *Cynips championi* Cameron de la que solo se conocía la agalla (Fig. 3H). Esta especie se ha redescrito y se ha transferido ahora al género *Odontocynips* Kieffer*,* que junto a *O. hansoni*, conocida previamente solo de Costa Rica, representan las primeras especies de *Odontocynips* citadas de Panamá (capítulo 2.5, Medianero *et al*., en prensa).

El resto de las especies inductoras de las agallas, aún no identificadas a nivel específico, se estima que son, en su gran mayoría, nuevas para la ciencia y están en procesos de estudio y descripción (Medianero y Nieves-Aldrey inédito).

Géneros representados en las muestras en proceso de estudio

Andricus Hartig. Se han encontrado representadas 12 morfoespecies inductoras de agallas en casi todas los organos de las plantas hospedantes.

Andricus sp.1, induce agallas globosas pluriloculares que deforman los amentos de *Q. salicifolia* (Fig. 5E). Colectada en la Carretera de Volcancito, El Salto, Alto Chiquero, Palmira y Volcán Barú.

Andricus sp.2, induce agallas crípticas en la base de las ramitas jóvenes de *Quercus bumelioides* (Fig. 2C). Colectada en el Volcán Barú.

Andricus sp.3, induce agallas caulinares conspicuas pluriloculares en los tallos de *Q. salicifolia* (Fig. 5F). Colectada en la Carretera de Volcancito, El Salto, Alto Chiquero y Volcán Barú.

Andricus sp.4, induce cecidias esféricas monotalámicas en las yemas de *Quercus bumelioides* (Fig. 2A). Colectada en el Volcán Barú.

Andricus sp.5, induce agallas crípticas en los tallos de *Quercus bumelioides* (Fig. 2B). Colectada en el Volcán Barú.

Andricus sp.6, induce agallas cónicas en las hojas de *Quercus lancifolia* (Fig. 4J).

Colectada en Piedra de Candela.

Andricus sp.7, induce agallas crípticas en los tallos de *Quercus bumelioides* (Fig. 2D). Colectada en el Volcán Barú.

Andricus sp.8, induce cecidias esféricas monotalámicas en las yemas de *Quercus insignis* (Fig. 4Q). Colectada en Bajo Mono.

Andricus sp.9, induce agallas crípticas en los tallos de *Quercus insignis* (Fig. 4R). Colectada en Bajo Mono.

Andricus sp.10, induce agallas hemisféricas en los tallos de de *Quercus lancifolia* (Fig. 4A). Colectada en Piedra de Candela.

Andricus sp.11, induce ensanchamiento conspicuos en los tallos de *Quercus lancifolia* (Fig. 4C). Colectada en Palmira.

Andricus sp.12, induce agallas crípticas en las bellotas de *Quercus lancifolia* (Fig. 4B). Colectada en Finca Hill.

El segundo género más abundante fue *Neuroterus* Hartig. Todas las especies de este género se encontraron induciendo agallas en especies de robles blancos (secc. Quercus).

Neuroterus sp.1, induce agallas cilíndricas pubescentes, muy numerosas en las hojas de *Quercus bumelioides* (Fig. 2O). Colectada en Volcán Barú, El Salto y en la Carretera de Volcancito.

Neuroterus sp.2, induce agallas esféricas sobre las hojas y tallos de *Quercus bumelioides* (Fig. 3D). Colectada en el Volcán Barú y en el Parque Internacional la Amistad.

Neuroterus sp.3, induce agallas crípticas en los tallos jóvenes de *Quercus bumelioides* (Fig. 2N). Colectada en el Volcán Barú.

Neuroterus sp.4, induce agallas subesféricas pluriloculares en el nervio medio de las hojas de *Quercus bumelioides* (Fig. 2K). Colectada en el Volcán Barú, en el Parque Internacional la Amistad y en Volcán.

Neuroterus sp.5, induce pequeñas cecidias de forma oval en las hojas de *Quercus bumelioides* (Fig. 2M). Colectadas en el Volcán Barú.

Neuroterus sp.6, induce agallas en las yemas foliares de *Quercus bumelioides* (Fig. 2L). Colectada en el Volcán Barú.

Neuroterus sp.7, induce agallas lenticulares en las hojas de *Quercus bumelioides* (Fig. 2P). Colectada en Volcán Barú y Piedra de Candela.

Neuroterus sp.8, induce agallas cilíndricas, muy numerosas en las hojas de *Quercus lancifolia* (Fig. 4G). Colectada en Finca Hill.

Neuroterus sp.9, induce agallas pluriloculares de consistencia dura en las yemas de *Quercus bumelioides.* Colectada en el Volcán Barú.

El tercer género con más especies fue *Dryocosmus* Giraud, las especies encotradas de este género en Panamá se caracterizan por inducir agallas en las hojas de las diferentes especies de *Quercus*.

Dryocosmus sp.1, induce cecidias lenticulares unidas por un punto muy fino a las hojas de *Quercus bumelioides* (Fig. 3B). Colectada en el Volcán Barú.

Dryocosmus sp.2, induce agallas vesiculares monotalámicas dispersas en las hojas de *Q. salicifolia* (Fig. 5G). Colectada en la Carretera de Volcancito y en el Volcán Barú.

Dryocosmus sp.3, induce agallas vesiculares irregulares, agregadas, en hojas de *Quercus bumelioides* (Fig. 3C). Colectada en el Volcán Barú.

Dryocosmus sp.4, induce cecidias piriformes, diminutas en hojas de *Quercus bumelioides* (Fig. 3G). Colectada en el Volcán Barú.

Dryocosmus sp.5, induce cecidias globosas irregulares, pluriloculares en hojas de *Quercus bumelioides* (Fig. 3F). Colectada en el Volcán Barú.

Dryocosmus sp.6, induce agallas cónicas pluriloculares en las hojas nuevas de *Quercus bumelioides* (Fig. 3A). Colectadas en la Carretera de Volcancito, El Salto, Alto Chiquero y en el Volcán Barú.

Dryocosmus sp.7, induce cecidias esféricas en el peciolo de las hojas de *Quercus lancifolia* (Fig. 4F). Colectada en Palmira.

Cuatro especies con características morfologicas afines al género *Cynips* Linnaeus fueron encontradas en las muestras, al igual que las especies del género *Neuroterus* todas induciendo sus agallas en especies de robles de la sección Quercus (robles blancos).

Cynips sp.1, induce agallas cónicas en el peciolo de las hojas de *Quercus bumelioides* (Fig. 3E). Colectada en el Volcán Barú, El Salto, Finca Hill y en la Carretera de Volcancito.

Cynips sp.2, induce cecidias esféricas en tallos de *Quercus bumelioides* (Fig. 2F). Colectada en el Volcán Barú.

Cynips sp.3, induce cecidias ovales en los tallos de *Quercus bumelioides* (Fig. 2H). Colectada en el Volcán Barú.

Cynips sp.4, induce cecidias esféricas algodonosas pluriloculares en hojas *Quercus lancifolia* (Fig. 4D). Colectadas en Cotito, Finca Hill y Piedra de Candela.

Una especie incluida en el género *Callirhytis* Forster fue colectada induciendo agallas globulares muy irregulares pluriloculares en el nervio medio de las hojas de *Q. salicifolia* (Fig. 5D). Colectada en la Carretera de Volcancito, Volcán Barú y Alto Chiquero.

Un porcentaje estimado en el 25% (11 agallas) de los 45 morfotipos de agallas de las cuales se obtuvo el adulto corresponden a formas sexuadas, mientras que de las restantes agallas solo se obtuvieron hembras y las evidencias morfológicas y fenológicas existentes apuntarían a que se trata de agallas de formas asexuales (ágamas).

Estimación de la riqueza de especies del área muestreada a partir de los muestreos realizados

Las curvas de acumulación de especies construidas con los estimadores no parametricos Jacknife 1, Jacknife 2 y Bootstrap basadas en los veinte meses de muestreo realizados en las 15 localidades ubicadas en la cordillera central de Panamá alcanzaron una leve asíntota y sugieren un número de agallas entre 76 y 95 para el área de estudio (Fig. 6).

Tribu Synergini

Se determinaron 11 especies de inquilinos en las 65 tipos de agallas colectadas, 10 especies pertenecen al género *Synergus*, de las cuales ocho son especies nuevas para la ciencia y dos especies, *Synergus nicaraguensis* Díaz & Gallardo y *S. mesoamericanus* Ritchie y Shorthouse conocidas de Nicaragua y Guatemala son citadas por vez primera para Panamá (Nieves-Aldrey & Medianero, 2011; capítulo 3.2 de esta memoria). Un nuevo género y una nueva especie; *Agastroroxenia panamensis* Nieves-Aldrey y Medianero ha sido descritas para la región (Nieves-Aldrey & Medianero, 2010; capítulo 3.1). El nuevo género de inquilinos descrito es el primero de este grupo trófico endémico de la región Neotropical.

Especies de *Quercus* anfitrionas

Los muestreos se efectuaron en ocho de las nueve especies de *Quercus* consideradas validas en Panamá (Tabla II), no se pudo colectar sobre *Q. costaricensis,* por lo inaccesible de la población. Nueve morfotipos de agallas inducidas por especies de los géneros *Amphibolips, Dryocosmus* y *Neuroterus* se colectaron sobre más de una especie de *Quercus*, sin embargo siempre pertenecientes a la misma sección del género. *Quercus bumelioides* y *Q. lancifolia* (secc. Quercus) son las especies que comparten más tipos diferentes de agallas con cinco en total. *Quercus bumelioides* con 35 morfotipos de agallas es la especie de *Quercus* que hospeda más especies de Cynipini, seguida de *Q. lancifolia* y *Q. salicifolia* está ultima de la sección Lobatae (Tabla II). De los 65 morfotipos de agallas colectadas 53% se encontraban en hojas, 37% en ramitas o ramas jóvenes producidas en la temporada, 4% en bellotas, 4% en yemas y 1% en amentos (Tabla II).

Riqueza por sitio de colecta

El Volcán Barú que representa el punto más alto de la Republica de Panamá con una altitud de 3.475 metros fue la localidad donde más agallas diferentes se colectaron (Tabla I). Otras localidades de importancia por su riqueza de agallas son Volcancito, El Salto (Distrito de Boquete) y las ubicadas en el corregimiento de Río Sereno (Distrito de Renacimiento) que es próximo a la frontera con Costa Rica (Tabla I). No se encontraron agallas en las poblaciones de *Quercus* que se encuentran en las localidades del centro y oriente del país: El Montuoso, Cerro Gaital y Cerro Chucanti (Fig. 1).

Tabla I. Datos geográficos de las localidades de muestreo en Panamá y número de morfotipos diferentes de agallas de Cynipidae colectados en cada una. El símbolo * indica las localidades que fueron visitadas una sola vez.

Provincia	Distrito	Localidad	Sitio	Coordenadas		Altitud (msnm)	No. De Agallas
Chiriquí	Boquete	Carretera de Volcancito	Entrada a Santa Lucia hasta	8°45′36.5"	82°26′30.2"	1188	17
			Finca Veggie	8°46′35.4"	82°27′42.6"	1450	
		El Salto	El Salto	8°47′32.8"	82°27′37.9"	1431	14
		Alto Quiel	Indiada	8°49′01.7"	82°28′32.3"	1600	2
		Bajo Mono	Bajo Mono	8°49′44.6"	82°28′37.1"	1547	3
		Alto Chiquero	Alto Chiquero	8°50′49.1"	82°29′18.4"	1869	3
		Jaramillo	Jaramillo Arriba	8°47′09.8"	82°25′14.0"	1253	1
		Palmira	Finca Castillo	8°43′49.6"	82°28′05.7"	1093	8
			Callas Verdes	8°45′26.0"	82°29′04.0"	1483	2
		Cerro Horqueta	Cerro Horqueta	8°49′25.5"	82°27′43.1"	1655	0
		Volcán Barú	Caseta de ANAM hasta	8°47′50.8"	82°29′35.9"	1808	45
			Nevera	8°46′36.8"	82°31′39.9"	3100	
	Renacimiento	Río Sereno	Cotito hasta Finca Hill	8°49′58.7"	82°44′44.5"	1270	15
			Piedra de Candela	8°52′47.2"	82°45′18.2"	1274	7
	Bugaba	Volcán	La Iglesia y San Benito	8°47′10.8"	82°49′03.8"	1379	1
		Cerro Punta	Parque Internacional la Amistad	8°53′21.18”	82°35′21.82	2371	3
			El Respingo	8°51′04.63”	82°32′02.55	2319	10
	Gualaca	Hornito	*Valle las Minas	8°39′51.0"	82°13′19.6"	1117	2
Coclé	Antón	EL Valle	*Cerro Gaital	8°37′2.4"	80°07′13.2"	821	0
Herrera	Las Minas	El Montuoso	*El Montuoso	7° 44′00.9”	80° 47′5.2”	718	0
Darién	Chepigana		*Cerro Chucanti	8°47′21.2"	78°27′06.7"	1437	0

Figura 2. Agallas colectadas sobre *Quercus bumelioides* (A-D): Agallas inducidas por especies indeterminadas del género *Andricus*, (E) Agalla de *Bassettia caulicola* Medianero & Nieves-Aldrey, (F-H) Agallas inducidas por especies indeterminadas de dos géneros no descritos afines al género *Cynips*, (I) Agalla de *Loxaulus championi* Medianero & Nieves-Aldrey, (J) Agalla de *Disholcaspis bettyannae* Medianero & Nieves-Aldrey, (K-P) Agallas inducidas por especies indeterminadas del género *Neuroterus*.

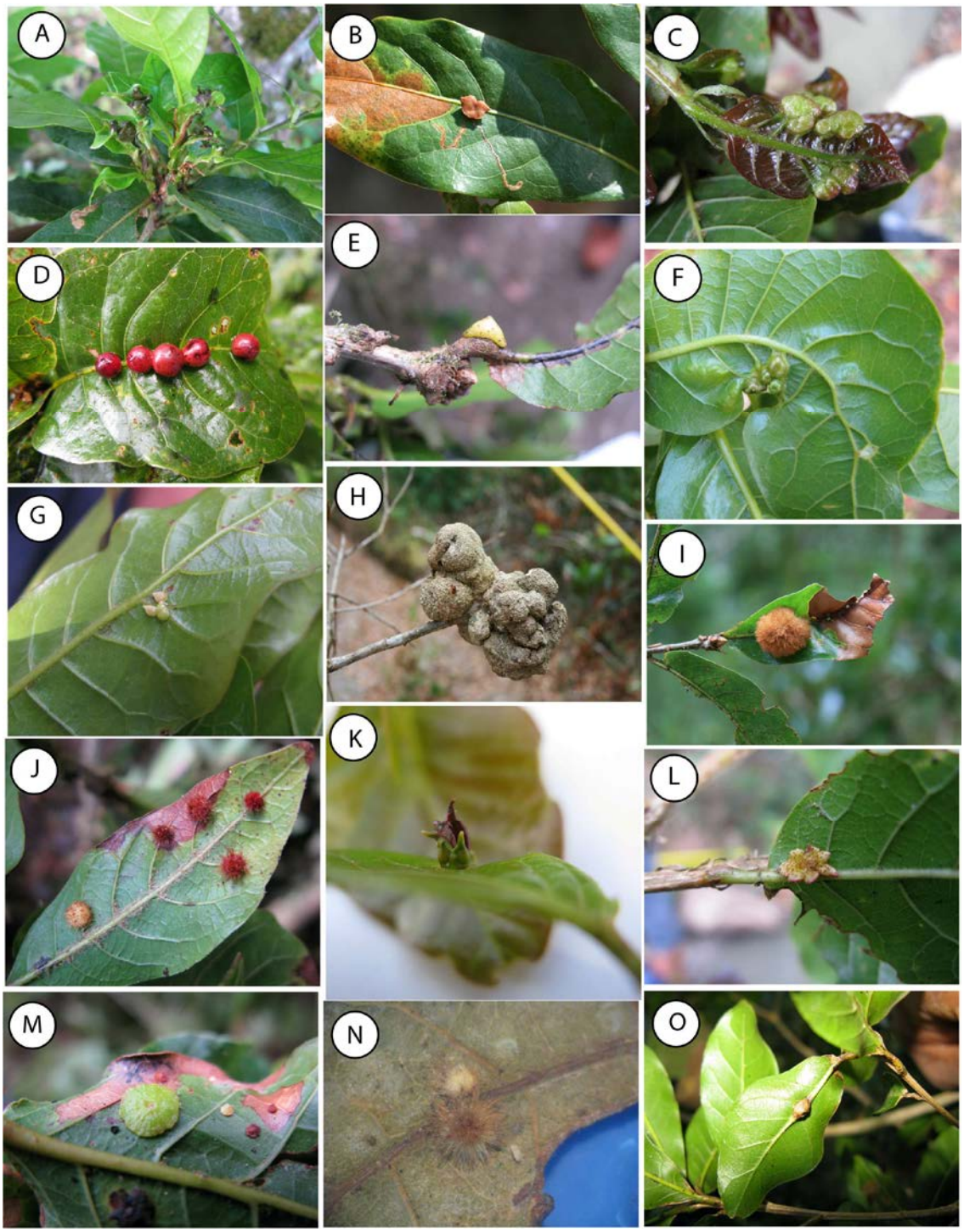

Figura 3. Agallas colectadas sobre *Quercus bumelioides* (A-G): Agallas inducidas por especies indeterminadas del género *Dryocosmus,* (H) Agalla de *Odontocynips championi* (Cameron), (I) Agalla de *Andricus guatemalensis* (Cameron), (J-O) Agallas inducidas por especies de géneros indeterminados de cinípidos.

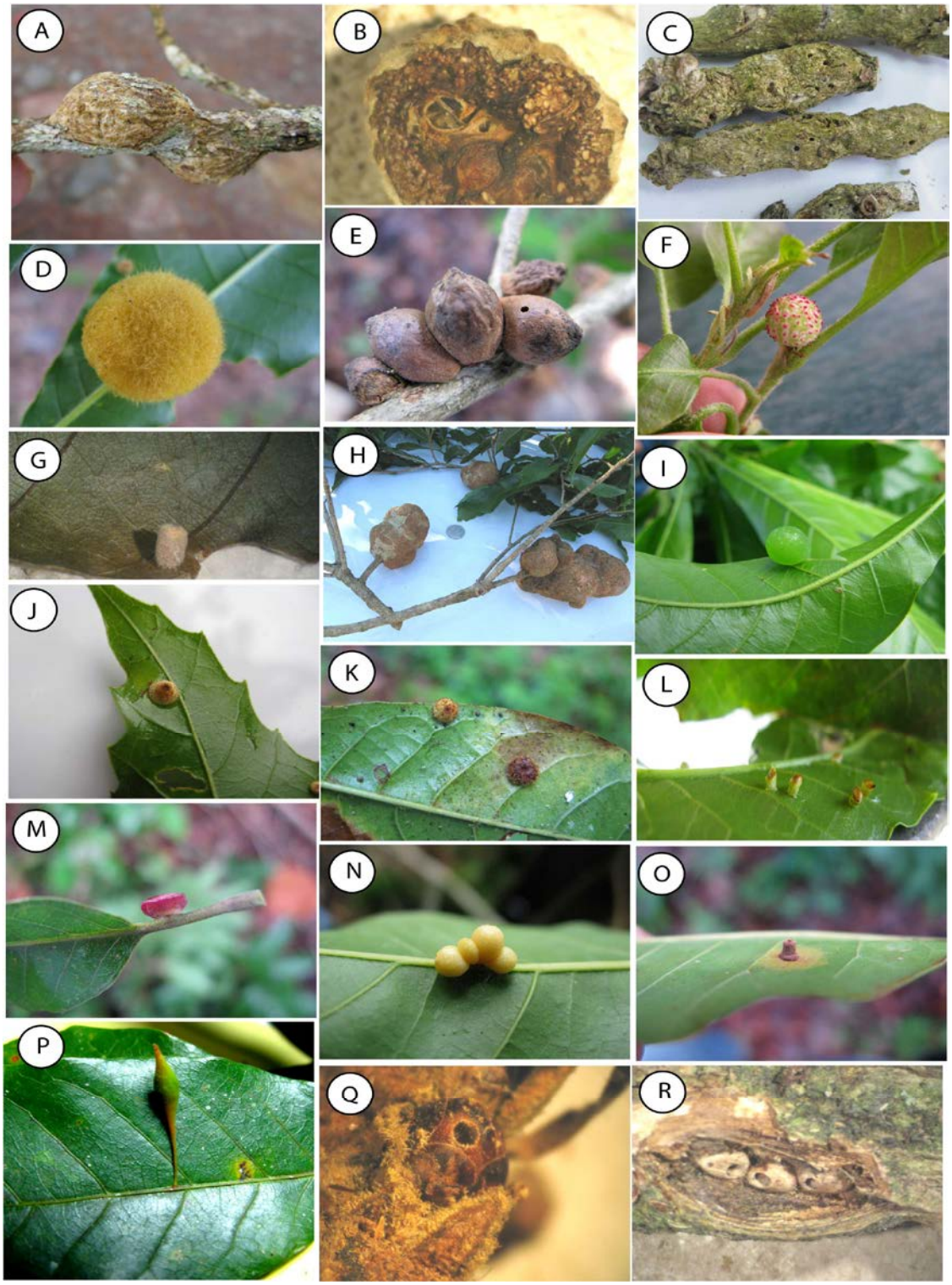

Figura 4. Agallas colectadas sobre *Q. lancifolia* (A-P) y *Q. insignis* (Q-R): (A-C) Agallas inducidas por especies indeterminadas del género *Andricus,* (D) Agalla de una especie del género *Cynips,* (E) Agallas de *Disholcaspis bisethiae* Medianero & Nieves-Aldrey, (F) Agalla inducida por una especie no identificada del género *Dryocosmus,*(G) Agalla inducida por una especie del género *Neuroterus,* (H) Agalla de *Odontocynips hansoni* Pujade-Villar, (I-P) Agallas inducidas por un cinípido inductor no determinado sobre *Q. lancifolia,* (Q-R) Agallas inducidas por especies indeterminadas del género *Andricus* sobre *Q. insignis.*

Figura 5. Agallas colectadas sobre *Quercus salicifolia*: (A-C) Agallas inducidas por especies del género *Amphibolips*: (A) de *A. castroviejoi*; (B) de *A. aliciae*; (C) de *A. salicifoliae*; (D) Agalla de una especie nueva del género *Callirhytis*, (E-F) Agallas de especies indeterminadas del género *Andricus*, (G) Agalla de una especie indeterminada del género *Dryocosmus*, (H-N) Agallas inducidas por cinípidos de géneros aún no identificados sobre *Q. salicifolia*.

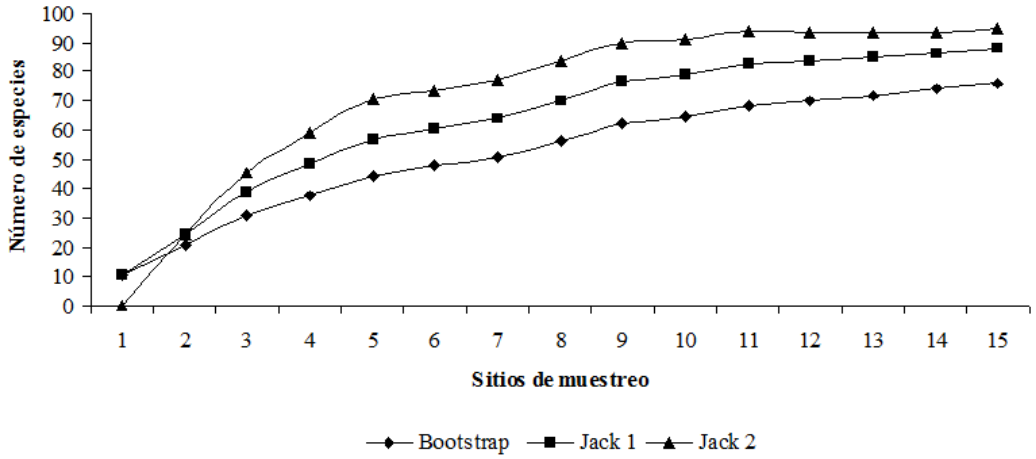

Figura. 6 Curva de acumulación de especies con los estimadores no parametricos Jacknife 1, Jacknife 2 y Bootstrap. Las curvas alcanzaron una leve asíntota y estiman un número de morfotipos de agallas entre 76 y 95 para el área de estudio

Parasitoides asociados a las agallas

Las agallas colectadas tienen una rica fauna de parasitoides asociados de diferentes familias de Chalcidoidea, la cual está aún casi por completo por estudiar. Entre los géneros más comunes destacan *Torymus* Dalman (Torymidae), *Eurytoma* Illiger, *Sycophila* Walker (Eurytomidae), *Eupelmus* Dalman (Eupelmidae), *Aprostocetus* Westwood (Eulophidae) y *Ormyrus* Westwood, (Ormyridae); este último género incluye tres especies: *O. venustus* Hanson, *O. unifasciatipennis* Girauld y *O. hegeli* Girauld, siendo esta última especie la primera vez que se cita en el Neotrópico y fue obtenida de agallas de *Disholcaspis bisethiae* en *Q. lancifolia,* en la localidad de Renacimiento próxima a la frontera con Costa Rica. Adicionalmente de las agallas han emergido tres especies de la superfamilia Ichneumonoidea; *Clistopyga moraviae* Gauld (Ichneumonidae), una especie del género *Bracon* Fabricius y otra del género *Psenobolus* Reinhard ambas de la familia Braconidae.

Tabla II. Especies de *Quercus* de Panamá muestreadas: número aproximado de individuos revisados por muestreo, número de agallas encontrados y su distribución por órgano de la planta.

Especie de *Quercus*	Sección	No. de individuos revisados por muestreo	No. de agallas encontradas	No. de agallas en hoja	No. de agallas en ramitas jóvenes	No. de agallas en bellotas	No. de agallas en amentos	No. de agallas en yemas
Q. salicifolia	Lobatae	300	14	4	7	2	1	
Q. benthamii	Lobatae	4	2	1	1			
Q. cortesii	Lobatae	3	3	1	2			
Q. gulielmi-treleasei	Lobatae	15						
Q. humboldtii	Lobatae	15						
Q. bumelioides	Quercus	275	33	19	12			2
Q. lancifolia	Quercus	200	20	14	5	1		
Q. insignis	Quercus	25	3	1	1			1

Tabla III. Géneros y número de especies de la tribu Cynipini identificados como inductores de agallas en Panamá. No se incluye dos especies de dos nuevos géneros encontrados, aún no descritos. .

Género del inductor	especies/morfoespecies	No. de Agallas en hoja	No. de agallas en ramitas o ramas jóvenes	No. de agallas en bellotas	No. de agallas en amentos	No. de agallas en yemas
Amphibolips	3	1	2			
Andricus	12	1	7	1	1	2
Bassettia	1		1			
Callirhytis	1	1				
Cynips	4	1	3			
Disholcaspis	2		2			
Loxaulus	2		1			
Dryocosmus	7	6	1			
Neuroterus	9	5	1			2
Odontocynips	2		2			

La fauna Neotropical de Cynipidae

Basándonos en nuestros resultados de campo y en la revisión de la literatura realizada, la fauna actual en el Neotrópico de la familia Cynipidae queda constituida por seis tribus, 18 géneros y 45 especies, 41 de las cuales son nativas y cuatro han sido introducidas en esta región biogeográfica (Tabla IV, Apéndice I).

Tabla IV. Relación de especies de Cynipidae citadas en la Región Neotropical y su distribución por país (Arg = Argentina; Chi = Chile; Col = Colombia; CRi = Costa Rica; Gua = Guatemala; Mex = México; Pma = Panamá; Nic = Nicaragua; Uru = Uruguay). Con * especies introducidas en la región.

Tribu	País	Referencia
Tribu Aylacini		
*Phanacis hypochoeridis**	Chi-Arg	Pujade-Villar & Díaz 2001
*Timaspis cichorii**	Chi	Nieves-Aldrey & Grez 2007
Tribu Cynipini		
Acraspis fugiensi	Gua	Kinsey 1936, Weld 1952
Amphibolips aliciae	Pma	Medianero & Nieves-Aldrey 2010a
Amphibolips castroviejoi	Pma	Medianero & Nieves-Aldrey 2010a
Amphibolips dampfi	Mex	Kinsey 1937b
Amphibolips salicifoliae	Pma	Medianero & Nieves-Aldrey 2010a
Andricus costaricensis	CRi	Melika *et. al.,* 2009
Andricus guatemalensis	Gua	Cameron 1883
Andricus imitator	Gua	Cameron 1883, Liljeblad & Ronquist 1998
Atrusca luminata	Gua	Kinsey 1936, Weld 1952
Atrusca lucaris	Gua	Kinsey 1936, Weld 1952
Bassettia caulicola	Pma	Medianero & Nieves-Aldrey 2010b
Disholcaspis bettyanne	Pma	Medianero & Nieves-Aldrey 2011
Disholcaspis bisethiae	Pma	Medianero & Nieves-Aldrey 2011
Loxaulus championi	Pma	Medianero *et al*. 2011a
Loxaulus panamensis	Pma	Medianero *et al.* 2011a
Odontocynips championi	Pma-Gua	Cameron 1883, Medianero *et al*. 2011b
Odontocynips hansoni	CRi-Pma	Pujade-Villar 2008, Medianero *et al.* 2011b
*Plagiotrochus amenti**	Arg	Weld 1952, Nieves-Aldrey & Grez 2007
Tribu Eschatocerini		
Eschatocerus acaciae	Uru	Dalla Torre & Kieffer 1910, Weld 1952
Eschatocerus myriadeus	Arg	Weld 1952
Eschatocerus niger	Arg	Weld 1952
Tribu Paraulacini		
Cecinothofagus gallaecoihue	Chi-Arg	Nieves-Aldrey *et al.* 2009
Cecinothofagus gallaelenga	Chi-Arg	Nieves-Aldrey *et al.* 2009
Cecinothofagus ibarrai	Chi-Arg	Nieves-Aldrey *et al.* 2009
Paraulax perplexa	Chi	Dalla Torre & Kieffer 1910
Paraulax queulensis	Chi	Nieves-Aldrey *et al.* 2009
Paraulax ronquisti	Chi	Nieves-Aldrey *et al.* 2009

Tabla IV. *continuación*

Tribu	**País**	**Referencia**
Tribu Pediaspidini		
*Pediaspis aceris**	Arg	Pujade-Villar & Díaz 2001
Tribu Synergini		
Agastoroxenia panamensis	Pma	Nieves-Aldrey & Medianero 2010
Synergus baruensis	Pma	Nieves-Aldrey & Medianero 2011
Synergus chiricanus	Pma	Nieves-Aldrey & Medianero 2011
Synergus colombianus	Col	Nieves-Aldrey 2005
Synergus cultratus	Gua	Ritchie & Shorthouse 1987
Synergus elegans	Pma	Nieves-Aldrey & Medianero 2011
Synergus filicornis	Gua	Cameron 1883
Synergus gabrieli	Pma	Nieves-Aldrey & Medianero 2011
Synergus kinseyi	Gua	Ritchie & Shorthouse 1987
Synergus laticephalus	Pma	Nieves-Aldrey & Medianero 2011
Synergus luteus	Pma	Nieves-Aldrey & Medianero 2011
Synergus mesoamericanus	Gua-Pma	Ritchie & Shorthouse 1987,
Synergus nicaraguensis	Nic-Pma	Díaz & Gallardo 1998
Synergus ramoni	Pma	Nieves-Aldrey & Medianero 2011
Synergus rufinotaulis	Pma	Nieves-Aldrey & Medianero 2011

Discusión

Los resultados obtenidos confirman la hipótesis inicial de este trabajo de que las especies de *Quercus* distribuidas por las montañas de Panamá albergan una rica fauna de especies de la familia Cynipidae. El número de géneros de la tribu Cynipini colectados en Panamá, (sin incluir los al menos dos nuevos géneros que se encuentran en proceso de estudio y descripción) es similar en diversidad a las cifras del continente Europeo. Los resultados de este estudio concuerdan con un escenario en el que, después de las dos ultimas glaciaciones en las que las especies de *Quercus* encontraron las condiciones climáticas adecuadas para distribuirse desde Norteamérica por el corredor montañoso de Centroamérica (Oh & Manos, 2008), y llegar hace unos 3. 400 años al altiplano de Santafé de Bogota (Kappelle, 1996), las poblaciones de Cynipini y sus inquilinos Synergini siguieron el patrón de distribución de sus plantas hospedantes, logrando establecerse y conformar una fauna comparable en diversidad a la de las regiones paleártica y neártica. Las montañas tropicales tienen una gran variedad de hábitat y climas a lo largo de su gradiente altitudinal lo que resulta en una marcada diferencia entre las tierras altas y las bajas. Debido a estas diferencias ambientales presentan, al igual que las islas, altos niveles de endemismo (Major, 1988). Estos niveles de endemismo se

han visto claramente reflejados en el caso de las poblaciones de Cynipidae de Panama aquí estudiadas. Por otra parte, estos mismos resultados indican que al menos en las montañas de Panamá, esta fauna ligada inevitablemente a las poblaciones de *Quercus*, se encuentra altitudinalmente muy aislada (entre 1000-3100 m), fraccionada y con la mayoría de la especies presentes en bajas densidades, debido a las actividades agropecuarias que se desarrollan en estas áreas y la creciente degradación y sustitución de los bosques montanos de *Quercus* por cultivos u otras formaciones vegetales. La ausencia de agallas en las áreas muestreadas del centro y oriente del país que hemos constatado en los muestreos de las poblaciones relictas de *Quercus* existentes en dichas áreas, sugiere extinciones locales de las especies debido a la fragmentación de las poblaciones de estas quercíneas (Fig. 1). Un elemento adicional que complica la situación de las poblaciones de *Quercus* y cinípidos en Panamá son los efectos del llamado calentamiento global, ya que estudios con polen realizados en la cordillera del Talamanca en Costa Rica indican que durante los últimos 18.000 años los bosques de *Quercus* se han desplazado a diferentes alturas en busca de las condiciones climáticas (principalmente temperatura) apropiadas para su desarrollo (Kappelle, 1996). Como en Panamá las poblaciones de *Quercus* crecen en los sitios de mayor altitud, cualquier aumento en la temperatura actual de la zona donde crecen estos árboles se convertiría en un factor limitante para el desarrollo de dichas especies arbóreas, lo que traería como consecuencia la pérdida de la mayor parte de la fauna asociada a estas especies incluyendo los cinípidos.

Los estimadores de riqueza potencial de especies que hemos usado en este trabajo, calculan la presencia de entre 76 y 95 especies de cinípidos para el área de estudio. Hay que matizar, sin embargo, que la cifra real será menor debido a la alternancia de generaciones; sexuada y asexuada que presentan las especies de la tribu Cynipini asociadas a fagáceas. Estas especies producen agallas, en cada una de las dos generaciones, casi siempre morfológicamente distintas. Cabe por ello pensar que algunos de los morfotipos de agallas atribuidos a especies distintas pudieran corresponder en realidad a dos morfotipos de las generaciones alternantes de una misma especie. Para poner en correspondencia los mencionados morfotipos sería necesario completar o cerrar los los ciclos biológicos de las especies, ya sea mediante experimentos de infección controlada, unido a más observaciones detalladas de campo, o mediante trabajos de marcadores moleculares, como los que se han realizado o se

vienen efectuando con especies paleárticas, mucho mejor conocidas. No cabe esperar, sin embargo, que dichos estos estudios de las especies panameñas puedan completarse a corto plazo.

Taxonómicamente los resultados también confirman la idea del uso inadecuado de caracteres morfológicos para la definición de los géneros de la tribu Cynipini (Dailey & Menke, 1980; Melika & Abrahamson, 2002; Liljeblad *et al*., 2008). Son muchas las homoplasias encontradas en las especies inductoras en este estudio, por lo que la clasificación dentro de un determinado género se convierte en una difícil tarea. En consecuencia solo en los casos donde existen sinapomorfias se ha decido proponer nuevos géneros. Lamentablemente las recientes sinonimias de muchos de los géneros de Cynipini del Neártico realizada por Melika & Abrahamson (2002), aunque buscaba ordenar la clasificación dentro de Cynipini, quedó incompleta y complicó más la situación ante la falta de información de las especies neotropicales. El mencionado trabajo necesita una mayor revisión ya que no contó con una adecuada revisión de todos los caracteres morfológicos (Melika *et. al.,* 2010).

De los géneros de Cynipini encontrados en este estudio cinco son de distribución exclusivamente americana, son los siguientes: *Amphibolips*, *Bassettia*, *Disholcaspis*, *Loxaulus* y *Odontocynips*. Los otros cinco géneros tienen representantes en otras zonas zoogeográficas del planeta, sin embargo géneros como *Andricus*, *Callirhytis*, *Neuroterus* son muy diversos en Norte América (Burks, 1979) lo que se refleja en nuestros resultados ya que los géneros *Andricus* y *Neuroterus* fueron de los más ricos en especies en Panamá. Dada su dificultad taxonómica, su estudio no ha podido ser abordado en este trabajo, quedando a la espera de su revisión en los próximos años.

Una aclaración especial merece la cita en Panamá del género *Cynips*. Kinsey (1936), incluyó tres especies colectadas en Guatemala dentro de este género, dos dentro del complejo *Dugesi* del subgénero *Atrusca* y otra dentro del complejo *Arida* del subgénero *Acraspis*. Weld (1952), le dio estatus de género a los subgéneros de Kinsey (1936), dejando el género *Cynips* (subgénero *Cynips* de Kinsey) restringido al Paleartico. Individuos obtenidos de cuatro morfotipos diferentes de agallas colectadas en Panamá presentan características morfologicas similares a especies del género *Cynips* sin corresponder a ninguno de los subgéneros de *Cynips* bajo el concepto de Kinsey o géneros de Weld. Futuros estudios deberán esclarecer si estos ejemplares deben atribuirse finalmente al género *Cynips* o uno o más géneros nuevos.

La presencia de los géneros *Bassettia* y *Loxaulus* en Panamá amplia considerablemente la distribución geográfica de estos géneros, los cuales solo habían sido citados de Estados Unidos (Medianero & Nieves-Aldrey, 2010b; Medianero *et al.,* 2011).

Conclusión final

Los datos obtenidos en este estudio permiten concluir que la distribución global de la familia Cynipidae, principalmente de las tribus Cynipini y Synergini, deberá ser revisada, ya que los escasos registros que se tiene de la familia en el Neotrópico se deben básicamente a falta de muestreos en la región y no a la ausencia de la familia en la misma. Los resultados también permiten concluir que las poblaciones de la familia Cynipidae al menos en Panamá son altamente vulnerables y se encuentran amenazadas de extinción debido a la fuerte presión que reciben por las actividades antropogénicas en las áreas donde crecen sus hospedadores obligados del género *Quercus.*

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Apéndice I. Especies de la familia Cynipidae citadas para la Región Neotropical

Superfamilia Cynipoidea Latreille 1802

Familia Cynipidae Latreille 1802

Subfamilia Cynipinae Latreille 1802

Tribu Aylacini Ashmead 1903

***Phanacis* Förster 1860**

Phanacis hypochoeridis Kieffer 1887. Introducida. Induce agallas caulinares conspicuas en los tallos de *Hypochoeridis glabra* (Asteraceae). Citada para Chile y Argentina (Pujade-Villar & Díaz, 2001, Nieves-Aldrey & Grez, 2007).

***Timaspis* Mayr 1881**

Timaspis cichorii Kieffer 1909. Introducida. Induce agallas crípticas en los tallos de *Cichorium intybus* (Asteraceae). Citada para Chile (Nieves-Aldrey & Grez, 2007).

Tribu Cynipini Latreille 1802

***Acraspis* Mayr 1881**

Acraspis fugiens Kinsey 1936. Induce agallas esféricas, algo ensanchadas en la base, en las hojas de *Quercus rugosa* (= *Q. decipiens*). Citada para Guatemala (Kinsey, 1936; Weld, 1952).

***Amphibolips* Reinhard 1865**

Amphibolips aliciae Medianero & Nieves-Aldrey 2010. Induce cecidias globulares en las ramitas de *Quercus salicifolia*. Citada para Panamá (Medianero & Nieves-Aldrey, 2010a).

Amphibolips castroviejoi Medianero & Nieves-Aldrey 2010. Induce cecidias globulares de 58 a 45 mm de diámetro en las ramitas de *Quercus salicifolia*. Citada para Panamá (Medianero & Nieves-Aldrey, 2010a).

Amphibolips dampfi Kinsey 1937. Induce agallas tipo "manzana" similar a la de *A. castroviejoi* en tallos de *Quercus ocoteaefolia*. Citado en Oaxaca, México (Kinsey, 1937b). Esta especie es la única en el área geográfica de México que corresponde a la

Región Neotropical.

Amphibolips salicifoliae Medianero & Nieves-Aldrey 2010. Induce cecidias globulares en las hojas de *Quercus salicifolia*. Citada para Panamá (Medianero & Nieves-Aldrey, 2010a).

***Andricus* Hartig 1840**

Andricus costaricensis Pujade-Villar & Melika 2009. Induce ensanchamientos conspicuos en los tallos de *Quercus costaricensis*. Representa la segunda especie de la tribu Cynipini citada para Costa Rica (Melika *et. al.,* 2009).

Andricus guatemalensis (Cameron 1883). Induce agallas algodonosas de forma esférica con la cámara larval muy lignificada en el nervio central de las hojas de *Quercus spp*. Citada para Guatemala y México (Cameron, 1883). Encontrada ahora también en Panamá. Estudios recientes sugieren que esta especie podría ser incluida en un nuevo género de la tribu Cynipini.

Andricus(=*Adleria*) *imitator* Cameron 1883. Induce agallas esféricas algodonosas de gran tamaño en las ramitas o pequeñas ramas de *Quercus sp*. Citada para Guatemala (Cameron, 1883; Liljeblad & Ronquist, 1998). Especie descrita solamente a partir de la agalla. Al igual que la anterior habría que incluirla en un nuevo género.

***Atrusca* Kinsey 1929**

Atrusca luminata Kinsey 1936. Induce cecidias esféricas monotalámicas unidas por un punto muy fino al nervio medio de las hojas de *Quercus rugosa* (= *Q. decipiens)*. Descrita y citada únicamente de Guatemala (Kinsey, 1936; Weld, 1952).

Atrusca lucaris Kinsey 1936. Induce cecidias esféricas monotalámicas más pequeña que la de la especie anterior, unidas por un punto muy fino al nervio medio de las hojas de *Quercus pilicaulis*. Al igual que la especie anterior citada únicamente de Guatemala (Kinsey, 1936; Weld, 1952).

***Bassettia* Ashmead 1887**

Bassettia caulicola Medianero & Nieves-Aldrey 2010. Induce agallas crípticas en los tallos de *Q. bumelioides.* Citada para Panamá (Medianero & Nieves-Aldrey, 2010b).

***Disholcaspis* Dalla Torre & Kieffer 1910**

Disholcaspis bettyannae Medianero & Nieves-Aldrey 2011. Induce agallas esféricas monotalámicas en forma de un brote con una cámara central en forma de huevo, en ramas de *Quercus bumelioides*. Citada para Panamá (Medianero & Nieves-Aldrey, 2011).

Disholcaspis bisethiae Medianero & Nieves-Aldrey 2011. Induce agallas subesféricas similar a la especie anterior, pero esta especie forma agregados de 10 o más agallas en los tallos de *Quercus lancifolia*. Citada para Panamá (Medianero & Nieves-Aldrey, 2011).

***Loxaulus* Mayr 1881**

Loxaulus championi Medianero & Nieves-Aldrey 2011. Induce agallas caulinares conspicuas en los tallos de *Q. bumelioides.* Citada para Panamá (Medianero *et al.,* 2011a).

Loxaulus panamensis Medianero & Nieves-Aldrey 2011. Induce agallas crípticas en los tallos de *Q. bumeliodes.* Citada para Panamá (Medianero *et al.,* 2011a).

***Odontocynips* Kieffer 1910**

Odontocynips championi (Cameron 1883). Induce agallas globulares muy irregulares en los tallos de *Quercus bumelioides*. Citada para Panamá y Guatemala (Cameron, 1883; Dalla Torre & Kieffer, 1910; Medianero *et al*., 2011b). Constituía la única especie citada para Panamá hasta 2010. Descrita sobre la base de agallas colectadas por George Champion en 1882 en las montañas de Chiriquí.

Odontocynips hansoni Pujade-Villar 2008. Induce agallas globulares, irregulares, pluriloculares en las ramas de *Quercus insignis* y *Q. lancifolia*. Se conoce de Costa Rica y Panamá (Pujade-Villar, 2008; Medianero *et al.,* 2011b). Esta especie fue la primera de

la tribu Cynipini citada para Costa Rica y la segunda del género *Odontocynips*.

***Plagiotrochus* Mayr 1881**

Plagiotrochus amenti Kieffer 1901 (= *P. suberi* Weld 1926). Introducida. Induce agallas crípticas en ramas de *Quercus robur* y *Q. suber*. Citada en los Estados Unidos y Argentina (Weld, 1926, 1952; Nieves-Aldrey, 1985, 2001; Pujade-Villar & Díaz, 2001; Nieves-Aldrey & Grez, 2007; Pujade-Villar *et al.,* 2008).

Tribu Eschatocerini Ashmead 1903

***Eschatocerus* Mayr1881**

Eschatocerus acaciae Mayr 1881. Induce agallas conspicuas, esferoides u ovoides en los tallos de *Acacia caven, A. farnesiana* y *Prosopis spp.* (Fabaceae). Citada para Uruguay (Dalla Torre & Kieffer, 1910; Houard, 1933; Weld 1952) y Argentina (Díaz & De Santis, 1975; Díaz, 1980).

Eschatocerus myriadeus Kieffer & Joergensen 1910. Induce agallas hemisféricas en los tallos de *Prosopis alpataco* y *P. campestris* (Fabaceae). Citada para Argentina (Houard, 1933; Weld, 1952; Díaz & De Santis, 1975; Díaz, 1980).

Eschatocerus niger Kieffer & Joergensen 1910. Induce cecidias globosas de 8-15 mm de diámetro en los tallos de *Prosopis alba*, *P. alpataco* y *P. campestris* (Fabaceae). Citado para Argentina (Houard, 1933; Weld, 1952; Díaz & De Santis, 1975; Díaz, 1980).

Tribu Paraulacini Nieves-Aldrey & Liljeblad 2009

***Cecinothofagus* Nieves-Aldrey & Liljeblad 2009**

Cecinothofagus gallaecoihue Nieves-Aldrey & Liljeblad 2009. Inquilino o parasitoide en agallas inducidas por *Aditrochus coihuensis* Ovruski (Pteromalidae) en yemas y tallos de *Nothofagus dombeyi* (Nothofagaceae). Citado para Chile y Argentina (Nieves-Aldrey *et al.,* 2009).

Cecinothofagus gallaelenga Nieves-Aldrey & Liljeblad 2009. Inquilino letal o

parasitoide en agallas inducidas por *Aditrochus fagicolus* Rübsaamen (Pteromalidae), en hojas de *Nothofagus pumilio* (Nothofagaceae). Citado para Chile y Argentina (Nieves-Aldrey *et al.,* 2009).

Cecinothofagus ibarrai Nieves-Aldrey & Liljeblad 2009. Inquilino o parasitoide en agallas inducidas por *Aditrochus coihuensis* Ovruski (Pteromalidae), en yemas de *Nothofagus dombeyi* (Nothofagaceae). Citado para Chile y Argentina (Nieves-Aldrey *et al.,* 2009).

***Paraulax* Kieffer 1904**

Paraulax perplexa Kieffer 1904. Especie de biología desconocida. Presumiblemente asociada a agallas inducidas en *Nothofagus obliqua* por especies del género *Espinosa* Gahan o *Aditrochus* Rübsaamen (Pteromalidae: Ormocerinae). Citada de Chile (Dalla Torre & Kieffer, 1910; Nieves-Aldrey *et al.,* 2009).

Paraulax queulensis Nieves-Aldrey & Liljeblad 2009. Especie de biología desconocida. Presumiblemente asociada a agallas inducidas por especies del género *Espinosa* Gahan en *Nothofagus obliqua*. Al igual que la anterior especie se conoce solo de Chile (Nieves-Aldrey *et al.,* 2009).

Paraulax ronquisti Nieves-Aldrey & Liljeblad 2009. Especie de biología desconocida. Descrita de Chile (Nieves-Aldrey *et al.,* 2009).

Tribu Pediaspidini Ashmead 1903

***Pediaspis* Tischbein 1852**

Pediaspis aceris Gmelin 1790. Introducida. Induce agallas en hojas de *Acer aff. campestre*. Citado para Argentina (Pujade-Villar & Díaz, 2001)

Tribu Synergini Ashmead 1896

***Agastoroxenia.* Nieves-Aldrey & Medianero 2010**

Agastoroxenia panamensis Nieves-Aldrey & Medianero 2010. Inquilino en agallas conspicuas inducidas por una especie indeterminada del género *Andricus* en los tallos de *Q. lancifolia.* Descrita de Panamá. (Nieves-Aldrey & Medianero, 2010).

***Synergus* Hartig 1840**

Synergus baruensis Nieves-Aldrey & Medianero 2011. Inquilino en agallas inducidas por una especie de *Callirhytis* en hojas de *Quercus salicifolia*. Citado para Panamá (Nieves-Aldrey & Medianero, 2011).

Synergus chiricanus Nieves-Aldrey & Medianero 2011. Inquilino en agalla inducidas por una especie de *Andricus* en yemas de *Quercus insignis*. Citado para Panamá (Nieves-Aldrey & Medianero, 2011).

Synergus colombianus Nieves-Aldrey 2005. Inquilino en agallas inducidas presumiblemente por una especie indeterminada de *Callirhytis* en bellotas de *Q. humboldtii*. Citada únicamente de Colombia (Nieves-Aldrey, 2005). Esta especie corresponde al único registro de la familia Cynipidae para Colombia.

Synergus cultratus Ritchie & Shorthouse 1987. Inquilino en agallas inducidas por "*Andricus brelandi*" en *Quercus pilicaulis*. Citado para Guatemala (Ritchie & Shorthouse, 1987).

Synergus elegans Nieves-Aldrey & Medianero 2011. Inquilino que ataca un amplio rango de cecidias inducidas por diferentes géneros como *Amphibolips, Disholcaspis* y *Cynips*. Citado para Panamá (Nieves-Aldrey & Medianero, 2011).

Synergus filicornis Cameron 1883. Inquilino en cecidias inducidas por *Andricus guatemalensis* en hojas de *Quercus mexicana*. Citado para Guatemala (Cameron, 1883).

Synergus gabrieli Nieves-Aldrey & Medianero 2011. Inquilino polífago que ataca agallas en hojas entre las que se encuentra las inducidas por *Andricus guatemalensis* y una especie no determinada del género *Neuroterus*. Citado para Panamá (Nieves-Aldrey & Medianero, 2011).

Synergus kinseyi Ritchie & Shorthouse 1987. Inquilino en agallas inducidas por *Andricus pereduros* en *Quercus pilicaulis*. Citado para Guatemala (Ritchie & Shorthouse, 1987).

Synergus laticephalus Nieves-Aldrey & Medianero 2011. Inquilino en una agalla (Fig. 5L) de una especie no determinada de cinípido inductor en ramas de *Q. salicifolia*. Citado para Panamá (Nieves-Aldrey & Medianero, 2011).

Synergus luteus Nieves-Aldrey & Medianero 2011. Inquilino en agallas crípticas inducidas por una especie del género *Loxaulus* en los tallos de *Quercus bumelioides*. Citado para Panamá (Nieves-Aldrey & Medianero, 2011).

Synergus mesoamericanus Ritchie & Shorthouse 1987. Inquilino en agallas inducidas por "*Andricus brelandi*" en *Quercus pilicaulis*, y en las de *Odontocynips championi* en *Q. bumelioides* Citado para Guatemala y Panamá (Ritchie & Shorthouse, 1987; Nieves-Aldrey & Medianero, 2011).

Synergus nicaraguensis Díaz & Gallardo 1998. Inquilino en agallas indeterminadas en el tallo de *Quercus oleoides*. Citado para Nicaragua (Díaz & Gallardo, 1998). Encontrada recientemente también en Panamá en agallas de *Disholcaspis bisethiae* (Nieves-Aldrey & Medianero, 2011).

Synergus ramoni Nieves-Aldrey & Medianero 2011. Inquilino en una agalla (Fig. 5I) de una especie no determinada de cinípido inductor en ramas de *Q. salicifolia*. Citado para Panamá (Nieves-Aldrey & Medianero, 2011).

Synergus rufinotaulis Nieves-Aldrey & Medianero 2011. Inquilino en agalla (Fig. 2F) de una especie no determinada del género *Cynips* en ramas de *Q. bumelioides*. Citado para Panamá (Nieves-Aldrey & Medianero, 2011).

CAPÍTULO 2

LOS CINÍPIDOS INDUCTORES DE AGALLAS EN ESPECIES DE *QUERCUS* (FAGACEAE): TRIBU CYNIPINI

OBJETIVO 2

Revisar taxonómicamente los géneros *Amphibolips*, *Bassettia, Disholcaspis*, *Loxaulus*, y *Odontocynips* (Cynipidae, Cynipini) de Panama, incluyendo la descripción de ocho especies nuevas.

2.1-El género *Amphibolips* Reinhard (Hymenoptera: Cynipidae: Cynipini) en el Neotrópico, con la descripción de tres especies nuevas de Panamá[2]

Resumen

Se describen tres nuevas especies de *Amphibolips* Reinhard 1865 de Panamá: *Amphibolips castroviejoi*, *A. aliciae*, y *A. salicifoliae* (Hymenoptera: Cynipidae: Cynipini). Las tres especies inducen agallas en *Quercus salicifolia* Née (Fagaceae, secc. Lobatae, robles rojos). Se dan datos sobre los caracteres diagnósticos, la distribución y la biología de las especies. Los límites genéricos de *Amphibolips* son revisados añadiendo nuevos caracteres morfológicos diagnósticos. Se discute la presencia del género *Amphibolips* en la región Neotropical. Las nuevas especies representan el primer registro del género para América Central.

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The genus *Amphibolips* Reinhard (Hymenoptera: Cynipidae: Cynipini) in the Neotropics, with description of three new species from Panama

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Abstract

Three new species of *Amphibolips* Reinhard 1865, *Amphibolips castroviejoi*, *A. aliciae*, and *A. salicifoliae* (Hymenoptera: Cynipidae: Cynipini) are described from Panama. The three new species induce galls on *Quercus salicifolia* Née (Fagaceae, sect. Lobatae, Red Oaks). Diagnostic characters, gall descriptions, distribution, and biological data are given. The generic limits of *Amphibolips* are re-established with adding new generic morphological characters. The presence of the genus *Amphibolips* in the Neotropical region is discussed. The new species represent the first record of this genus from Central America.

Key words: Cynipidae, oak gall wasps, *Quercus*, Panama

Introduction

Amphibolips Reinhard is a morphologically and biologically distinctive, well-defined, genus of oak gall wasps (Cynipidae: Cynipini). The genus includes some of the largest known adult gallwasps and "oak apple" galls (female > 6.5 mm; gall 70 mm in diameter) (Beutenmüller 1909). The known range of this genus extends from Canada to Mexico (Dalla Torre & Kieffer 1910; Weld 1952) and is thus classified as Nearctic

(Liljeblad *et al.* 2008). Although Melika & Abrahamson (2002) erroneously reported that the genus was also present in Central America, it is certain that one species, *A. dampfi* Kinsey 1937, was observed in Oaxaca (southern Mexico), a geographic area belonging the Neotropical region.

According to Liljeblad *et al*. (2008), there are 40 known species in the Nearctic region: 29 from regions north of Mexico (United States and Canada) (Burks 1979; Melika & Abrahamson 2002) and 11 from Mexico (Bassett 1890; Beutenmüller 1911; Kinsey 1937). Before 1937, only two species of the genus *Amphibolips* were recorded in Mexico (*A. palmeri* Bassett 1890 and *A. nigra* Beutenmüller, 1911). Kinsey (1937) described nine additional species from Mexico; seven species, represented only by asexual forms, which were included in the "*Niger* Complex": *A. gumia* Kinsey, *A. jubatus* Kinsey, *A. elatus* Kinsey, *A. maturus* Kinsey, *A. nebris* Kinsey, *A. niger* Beutenmüller (=*A. nigra*) and *A. pistrix* Kinsey, a typical Mexican group with a unique representative in southern Arizona (Kinsey 1937). The other three species present in Mexico are *A. dampfi* Kinsey, *A. nassa* Kinsey and *A. fussus* Kinsey. Until now, the most recently described species of *Amphibolips* was *Amphibolips murata* Weld 1957, recorded from Florida.

According to Melika & Abrahamson (2002) the morphological characters of adults and their galls are very uniform in *Amphibolips.* These authors stated that the morphology of the sexual and asexual female is identical; however at least the asexual females of the *Niger* complex differ from sexual females of *Amphibolips* species in number of antennal segments (Kinsey 1937). Diagnostic characters of *Amphibolips* include antennae presenting 12-14 segments in females and 15-16 segments in males, very robust and coarsely rugose mesosoma and head; scabrous or aciculated, distinct or indistinct notauli more or less obliterated by the rugosities or coarse sculpture of mesoscutum; scutellum usually emarginate at the posterior end, with very large, deep, and wrinkled scutellar foveae; smooth or punctate metasomal tergites; metatarsal claws with strong basal lobes; forewings that are usually more or less smoked and exhibit a fuliginous cloud, bands, or are almost entirely fuliginous; a radial cell open at the anterior margin; and a narrow, needle-like, long projecting portion of the ventral spine of the hypopygium that is usually more robust and broader that in the closely allied genus *Andricus* Hartig (Beutenmüller 1909; Melika & Abrahamson 2002). Both sexual and asexual generations of *Amphibolips* species induce stem, bud and leaf galls (Melika

& Abrahamson 2002). Galls of the species of this genus are characteristically of the spongy oak-apple type, usually globose or spindle-like. All known species induce monolocular galls; they contain a single central cell in a spongy, soft parenchima tissues; at other times, the interior of the gall is almost empty and the single central cell is supported by radiating filaments (Beutenmüller 1909; Kinsey, 1937).

Phylogenetically, *Amphibolips* was recovered as related to some Nearctic species of *Andricus,* especially to *Andricus hastatus* (formerly *Erythres* Kinsey) (Liljeblad *et al.* 2008). However unpublished molecular results seems challenge this hypothesis (Melika pers. comm.). Six species of North American *Andricus* were recently transferred to *Amphibolips* by Melika & Abrahamson (2002), but the genus has not been fully revised, though the effort is badly needed.

This paper contains the first report of the genus *Amphibolips* in Central America and includes the description of three new species from Panama. For the first time, in *Amphibolips* description of the new species' morphological characters is based on scanning electron microscopy, allowing a better illustration of some traditional characters, their use in the identification key or the discussion of some new diagnostic characters of the genus, as the shape of the metatarsal claw.

Material and methods

Study material. The adults studied were reared from galls collected on *Quercus salicifolia* Née. Samplings were made and material was collected from December 2007 to May 2009 at Volcan Baru and Boquete, Chiriqui Province, Panama. The adult insects emerged from the galls in rearing cages under laboratory conditions.

Specimen preparation. For observation under a scanning electron microscope (SEM), adult cynipids were dissected in 70% ethanol, air dried, mounted on a stub and coated with gold. Micrographs were taken with an EVO 40 Zeiss and FEI QUANTA 200 (high vacuum technique) for several standardized views. Forewings were mounted in Euparal on slides and later examined under a Wild MZ8 stereo microscope. Representatives of some species with poor representation in the samples were not dissected but instead directly observed using the same SEM at low vacuum (voltage) technique, without coating. Images of adult habitus and gall dissections were taken with

a NIKON Coolpix 4500 digital camera attached to a Wild MZ8 stereo microscope. Measurements were made with a calibrated micrometer scale attached to an ocular of the light microscope. Terminology of morphological structures and abbreviations follow Ronquist & Nordlander (1989), Ronquist (1995), Nieves-Aldrey (2001) and Liljeblad *et al.* (2008).

Results

Amphibolips castroviejoi Medianero & Nieves-Aldrey sp. nov.

(Figs.1, 2, 7C, 7F & 8 A-C)

Type material. Holotype ♀ (Fig. 7A) (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. Cat. nº 2022). PANAMA, Chiriquí, Carretera de Volcancito, Boquete 8º 43' 23 07" N, 82º 27' 19 07" W, 1404 m; ex gall on twigs of *Quercus salicifolia* Née (Fagaceae), gall collected 28.i.2008, insect emerged ii.08, E. Medianero leg. Paratypes: 1♂ same data as holotype; 1♀, 1♂: same data as holotype, but collected 12.i.2008, insect emerged i.08. One paratype in MNCN, two paratypes in Maestría en Entomología, Universidad de Panamá (MEUP).

Additionally, 1♀ paratype of the type series was dissected for SEM observation (in MNCN.

Etymology. Named after Dr. Santiago Castroviejo, dear colleague and friend, a recently deceased eminent botanist who worked for many years in the Flora of Coiba National Park (Panama).

Diagnosis and comments. Closely allied to *A. dampfi* Kinsey, from Mexico, being similar in color and a majority of morphological characters. Males of the two species share a similar forewing coloration pattern, which is almost entirely smoky, with a clear crossing band extending from the radial cell to the discoidal cell. The species differ mainly in the sculpture of the thorax. *A. dampfi* have a very coarse sculpture, forming a series of small, rectangular spaces (Kinsey 1937: p. 429), whereas the sculpture of the thorax is very irregular, even shapeless, in *A. castroviejoi*. The new species has a wide band extending across the forewing from the tip of radial cell to posterior part the apical margin (Fig.7C), whereas the band does not extend as far across the ventral margin of the wing in *A. dampfi*

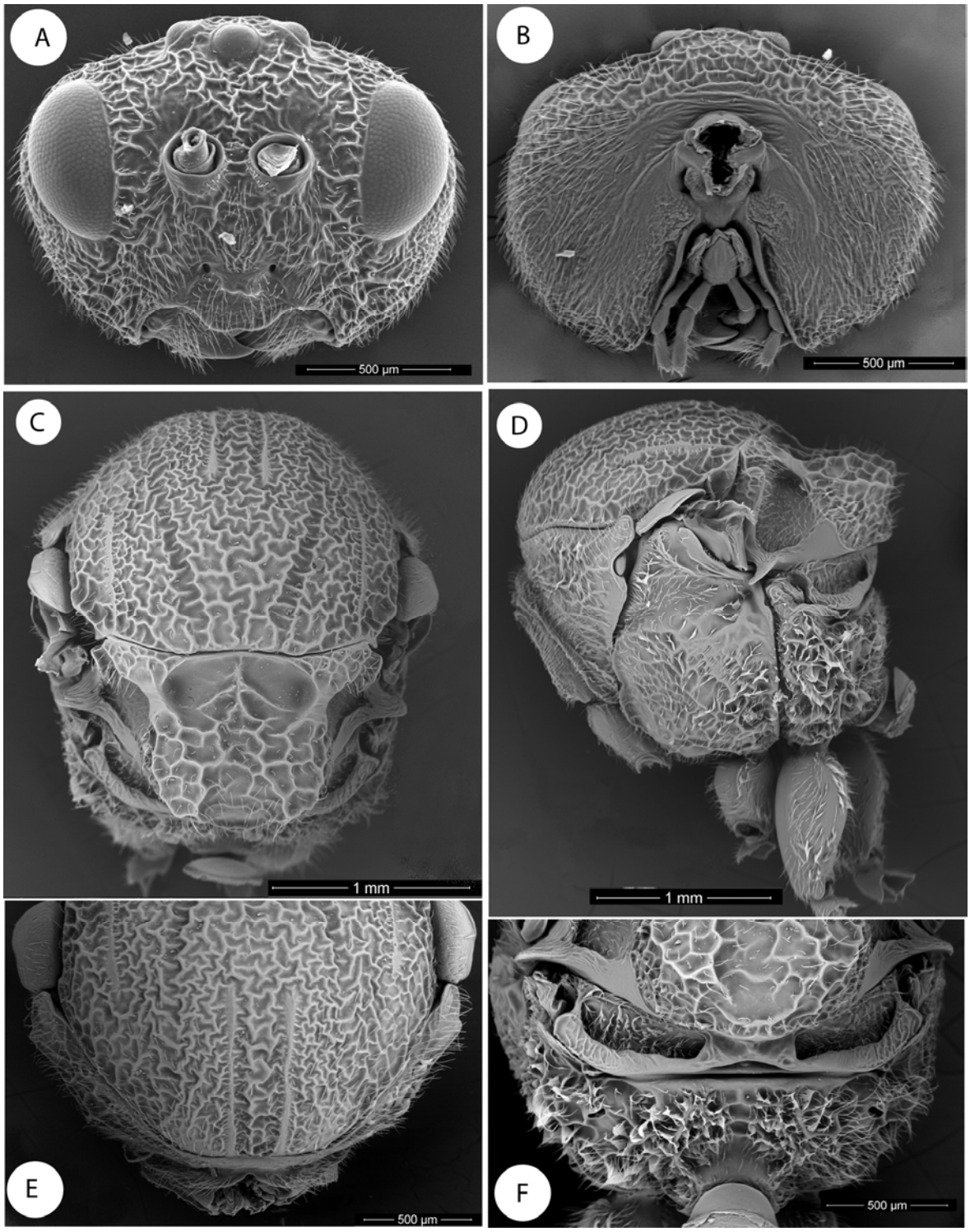

Figure 1. *Amphibolips castroviejoi*: (A) Head anterior view. (B) Head posterior view. (C) Mesosoma dorsal view. (D) Mesosoma lateral view. (E) Pronotum antero-dorsal view. (F) Propodeum.

(Kinsey, 1937). Additionally, *A. castroviejoi* have complete notauli, only lost in the coarse surface in anterior one third, and the anteroadmedian signa visible. In *A. dampfi*, the notauli are indicated but nearly lost in sculpture and the anteroadmedian signa are less visible.

Description. Body length (measured from anterior margin of head to posterior margin of metasoma) 5.0 mm (N = 2) for females; 4.45 mm (range 4.33-4.58; N = 2) for males. Head and mesosoma of female shiny and black. Metasoma, clypeus, mandibles, antenna and legs rufo-piceous; with scape, pedicel, F1, F2, coxae and femora more darkened. Forewing almost entirely and very heavily smoky, especially in medial half of basal and radial cells, with a wide clear band extending across wing from tip of radial cell to the apical area between the medial and cubital veins; small clear clouds present on Cu-a and R1 +Sc. Male with coloration similar to female, but legs uniformly rufo-piceous.

Female. Head, coarsely rugose, pubescent; in dorsal view about 2.6 times wider than long. POL 1.1 times longer than OOL, posterior ocellus separated from inner orbit of eye by 2.5 times its longest diameter. Head in anterior view (Fig. 1A) transversely ovate, 1.29 times wider than high, gena slightly broadened behind eye. Vertex, frons, lower face, gena, and occiput with strong reticulate-rugose sculpture, irradiating carinae from clypeus not discernible; head moderately pubescent, with relatively long setae, except vertex and frons with sparse and shorter setae. Clypeus trapezoid, 1.5 times wider than high, shiny and smooth, moderately pubescent, ventral margin strongly projecting over mandibles and slightly sinuate. Anterior tentorial pits well visible; epistomal sulcus and clypeo-pleurostomal lines slightly distinct. Malar space 0.6 times height of compound eye. Toruli situated slightly below mid-height of compound eye; distance between antennal rim and compound eye 0.7 times width of antennal socket including rim. Ocellar plate slightly raised. Occipital carina lacking; strong transverse wrinkles present on occiput. A carina, dorso-laterad to occipital foramen, present, which is long and continues ventrally past posterior tentorial pits. Gula short; distance between occipital and oral foramina less than height of occipital foramen (Fig. 1B). Hypostomal sulci well separate at oral fossa.

Mouthparts (Fig. 1B): mandibles strong, exposed; with dense setae in base, right mandible with three teeth; left with two teeth. Cardo of maxilla not visible, maxillary stipes about 3.3 times longer than wide. Maxillary palp five-segmented. Labial palp

three-segmented.

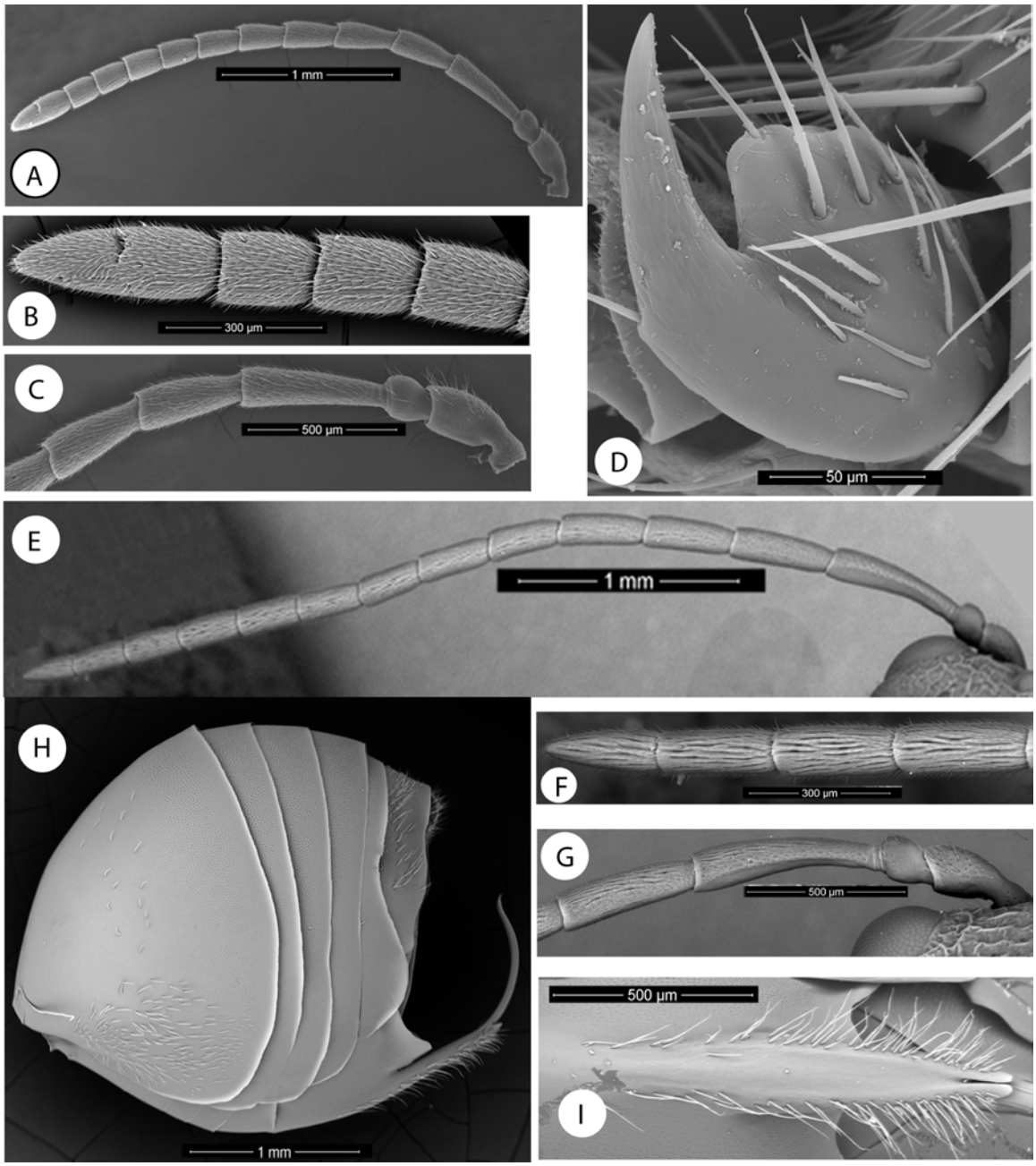

Figure 2. *Amphibolips castroviejoi*: (A) Female antenna. (B) Detail of last flagellomeres. (C) Detail of basal flagellomeres. (D) Metatarsal claw. (E) Male antenna. (F) Detail of terminal flagellomeres of male antenna. (G) Detail of basal flagellomeres male antenna. (H) Metasoma lateral view. (I) Detail of ventral spine of hypopygium.

Antenna (Fig. 2A), of moderate length, as long as 1/2 body length; with 13 antennomeres; flagellum not broadening towards apex; with relatively long, erect setae, and elongate placodeal sensilla hardly visible (Fig. 2B). Relative lengths of antennal segments: 17:12:38:26:25:22:19:18:16:15:15:13:28. Pedicel (Fig. 2C), globose, small, 0.7 as long as scape; F1 1.4 times as long as F2. F6-F10 longer than wide, F11 2.7 times longer than wide, 2.1 times as long as F10 (Fig. 2B). Placodeal sensillae on F8-F11 disposed in one row of 2-4 sensillae in half dorsal area of each flagellomere.

Mesosoma. Strongly, coarsely rugose, in lateral view as high as long. Pronotum, moderately pubescent; lateral surface of pronotum with strong rugose sculpture; moderately pubescent, with relatively long setae. Ratio of length of pronotum medially/laterally = 0.24. Pronotal plate indistinct dorsally (Fig. 1E).

Mesonotum (Fig. 1C). Mesoscutum barely pubescent and with strong rugose-reticulate sculpture. Notauli distinct posteriorly and medially, broad and convergent posteriorly, crossed by transversal rugose sculpture; median mesoscutal impression indistinct, lost in the coarse sculpture. Anteroadmedian signa clearly visible. Transscutal fissure narrow, well-visible, deeply impressed. Scutellar foveae ellipsoidal, deep, about 1/3 as long as scutellum, smooth and separated by a septum; their anterior and posterior margins marked. Scutellum (Fig. 1C) subquadrate from above, about 0.4 as long as mesoscutum, strongly reticulate-rugose and deeply emarginate at posterior margin, emargination reaching posterior one third of scutellum length; in lateral view extending posteriorly slightly over the dorsellum. Axillula moderately pubescent, their anterior and posterior margins marked. Mesopleuron coarsely rugose and moderately pubescent, excepting the posterodorsal area (Fig. 1D).

Metanotum (Fig. 1F). Metapectal-propodeal complex. Metapleural sulcus reaching posterior margin of mesopectus at about mid-height of metapectal-propodeal complex (Fig. 1D). Lateral propodeal carinae indistinct, slightly divergent anteriorly, (Fig. 1F). Median propodeal area rugose and densely pubescent. Nucha rugose.

Legs. Densely pubescent; femora and tibiae robust; metatarsal claws with strong triangular basal lobe or teeth (Fig. 2D).

Forewing (Fig. 7C): As long as body, radial cell 3.4 times longer than wide; open along anterior margin; areolet small, ovoid, closed and distinct. R1, Rs and M nearly straight, not reaching wing margin. Rs+M reaching basalis at its mid-height. First abscissa of radius (2r) and 2r-m curved. Apical margin with short hair fringe.

Metasoma (Fig. 2H), large as long as head and mesosoma combined, in lateral view as high as wide. Second metasomal tergite covering about two third of metasoma, with band of micropuntures clearly visible in posterior one third; punctures visible on subsequent tergites; ventral area of second metasomal tergite moderately pubescent. Projecting part of hypopygial spine long (Fig. 2I); about 3 times as long as wide in ventral view; laterally with long setae, longer than spine width but not forming an apical patch.

Male (Fig. 7B). Similar to female except as follows: Antenna with 13 flagellomeres (Fig. 2E); F1 slightly curved, posteriorly flattened and expanded apically (Fig. 2G). Placodeal sensillae present on flagellomeres 1-13, increasing in number towards apex (Fig. 2F). Relative length of antennomeres: 15:9:35:27:23:23:19:19:17:17:17:16:15:14:13. Metasoma smaller than in female; T2 0.7 of metasoma length.

Gall (Fig. 8A-C). , Irregularly spherical or globose, a bit elongated at its basis, monothalamic, with smooth and mottled surface. Light green when fresh (Fig. 8A) and light cream when mature (Fig. 8B); the outer shell is thin but firm. Internally it is of a soft, uniformly spongy consistence, filling the entire gall (Fig. 8C). The larval cell is rounded and is embedded in the soft internal substance. Diameter 58 to 45 mm (on average 54 x 43 mm). Formed in twigs of *Quercus salicifolia* Nee. The gall most closely resembles that of *Amphibolips murata* Weld, 1957 known from Florida (USA).

Distribution. *A. castroviejoi* was found between 1000-2681 m a.s.l. at Chiriqui, Panama.

Biology. Only the sexual generation is known, inducing galls on *Quercus salicifolia* and likely on other *Quercus* species (section Lobatae). The galls are found between December and May, during the dry season in Panama. The insects studied emerged in January and February.

Amphibolips aliciae **Medianero & Nieves-Aldrey sp. nov.**
(Figs. 3, 4, 7D-E & 8D-F)

Type material. Holotype ♀ (Fig. 7D) (in Museo Nacional de Ciencias Naturales, Madrid, Spain, card mounted. Cat nº 2023). PANAMA, Chiriquí, Carretera de Volcancito, Boquete 8º 46' 23 7" N, 82º 27' 19 7" W, 1404 m; ex gall on twigs of *Quercus salicifolia* Née (Fagaceae), gall collected 25.i.2009, insect emerged 25.i.09, E. Medianero leg. Paratypes: 2♂, same data as holotype, but one ♂ ex gall collected 12.i.2008, insect emerged ii.08, E. Medianero leg. One paratype in MNCN, one paratype in Maestría en Entomología, Universidad de Panamá (MEUP).

Etymology. Named after our good friend, the botanist Alicia Ibañez, in memory of unforgettable field sampling experiences in Panama.

Diagnosis and comments. *Amphibolips aliciae* is characterized by complete notauli, broad posteriorly; sub-quadrate deep scutellar foveae; the scutellum only slightly emarginated posteriorly, micropunctures on metasomal T3 very faint, hypopygial spine long; wings are not heavily smoked, only with a smoky brown patch at the base of the radial cell. The new species closely resembles *A. castroviejoi* in coloration, and most morphological characters but differs in some features as stated in the identification key, especially in the morphology of mesoscutum and scutellum and coloration of forewings. Furthermore, the inner structure of their respective galls is different. From the related sexual forms described by Kinsey from Mexico (Kinsey, 1937), *A. aliciae* is readily distinguishable mainly by less heavily infuscate forewing. By this late morphological character, the new species resembles some Nearctic species of *Amphibolips,* namely *A. melanocera* Ashmead, 1885; *A. cookii* Gillette, 1888; *A. globulus* Beutenmüller, 1909; *A. acuminata* Ashmead, 1896, but differs from all of them by distinct combinations of several features, such as type of gall, legs and metasoma coloration, mesoscutum and scutellum sculpture type, shape and sculpture of the scutellar foveae, number of male antennal segments, and other morphological characters (Beutenmüller 1909).

Description. Female. Body length (measured from anterior margin of head to posterior margin of metasoma) 4.58 mm (N = 1) for females; 4.08 mm (range 4.0-4.16; N = 2) for males. Head and mesosoma of female shiny and black. Metasoma, reddish brown. Antenna black with five last flagellomeres clearer. Legs black, with tibiae dark

brown and tarsi light brown. Forewing slightly smoky brown, with veins dark brown and large brown patch at base of radial cell. Male with coloration similar to female.

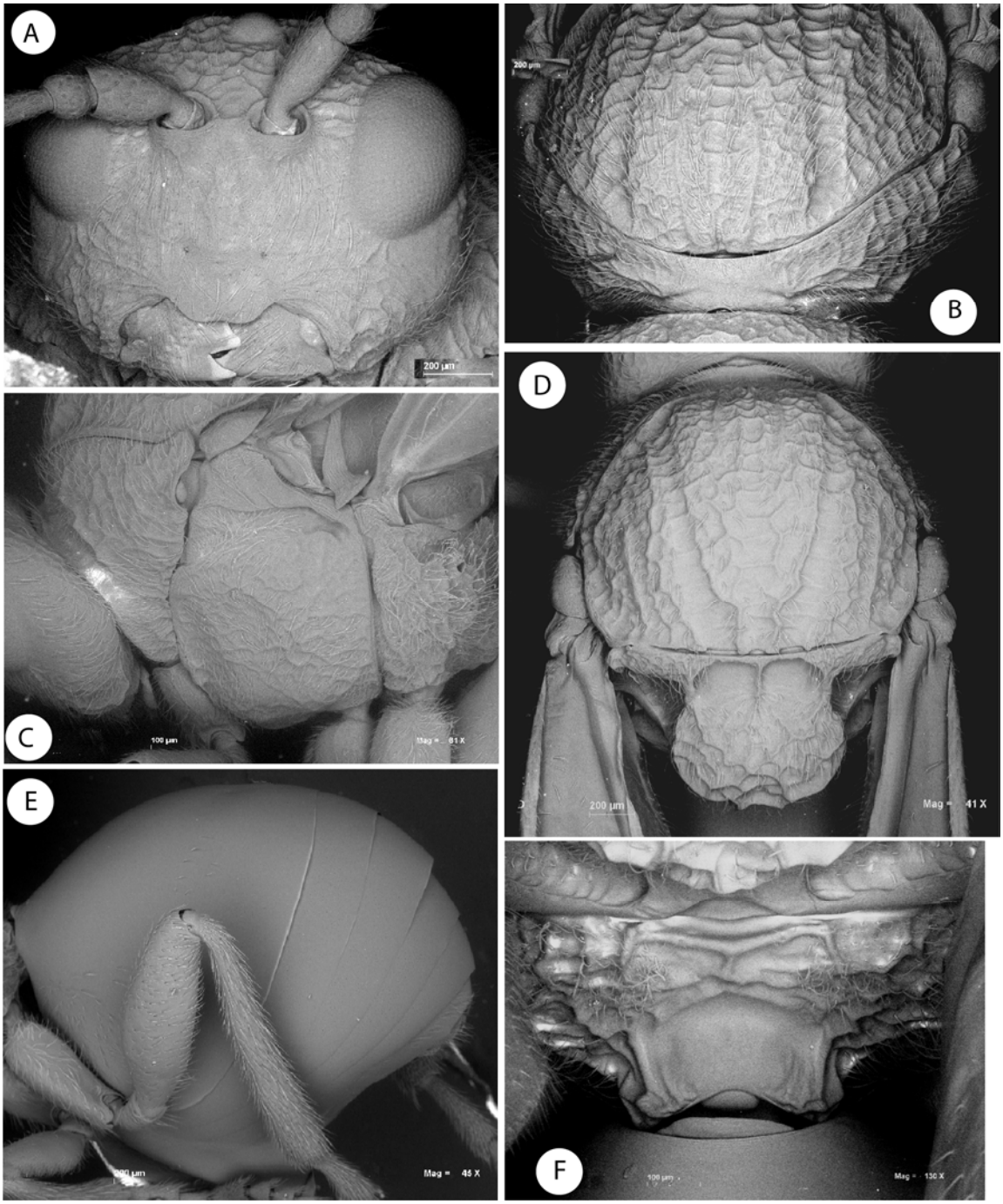

Figure 3. *Amphibolips aliciae*: (A) Head anterior view. (B) Pronotum anterior view. (C) Mesosoma lateral view. (D) Mesosoma dorsal view. (E) Metasoma lateral view. (F) Propodeum.

Female. Head, coarsely reticulate-rugose, pubescent, in dorsal view about 3 times wider than long. POL 0.8 times longer than OOL, posterior ocellus separated from inner

orbit of eye by 2.2 times its longest diameter. Head in anterior view (Fig. 3A) more or less oval, 1.17 times wider than high. Genae slightly expanded, mostly smooth and pubescent. Vertex, frons, face, and occiput reticulate-rugose, moderately pubescent. Clypeus, trapezoidal, smooth and moderately pubescent; ventral margin projecting over mandibles, its margin slightly sinuate. Anterior tentorial pits visible; epistomal sulcus and clypeo-pleurostomal lines indistinct; some irradiating strigae from clypeus visible, although obscured by coarse sculpture. Malar space 0.6 times height of compound eye. Distance between antennal rim of torulus and compound eye 0.6 times width of antennal socket including rim. Ocellar plate not raised. Mouthparts. Mandibles strong, exposed, with dense setae in base.

Antenna (Fig. 4A) as long as 1/2 body length; with 11 flagellomeres; flagellum not broadening towards apex; with erect setae and elongate placodeal sensilla visible on F2–F11, placodeal sensillae increasing in number towards apex, on F6-F11 closely arranged in two rows (Fig. 4C); 1-2 pores visible on apex of F4–F10 (Fig. 4C). Relative lengths of antennal segments: 22:16:52:32:19:16:12:15:15:15:15:15:35. Pedicel, globose, small, 0.7 as long as scape; F1 1.6 times as long as F2 (Fig. 4B). F6-F10 longer than broad; ultimate flagellomere 2.5 times longer than broad, 2.3 times as long as F10.

Mesosoma. In lateral view as high as long, with strong coarse rugose sculpture. Pronotum (Fig. 3B), densely pubescent and with strong coarse sculpture in lateral areas. Ratio of length of pronotum medially/laterally = 0.3. Pronotal plate indistinct.

Mesonotum. Mesoscutum (Fig. 3D), moderate and uniformly pubescent, with strong reticulate-rugose sculpture. Notauli, complete, deep and wide, wider and strongly converging posteriorly, crossed by transversal rugae of the mesoscutum sculpture. Median mesoscutal impression faint in the coarse sculpture. Anteroadmedian signa visible. Transscutal fissure straight, narrow. Scutellum (Fig. 3D), rounded, narrower basally, about 0.3 as long as mesonotum, strongly reticulate-rugose and slightly emarginate at tip, moderately pubescent. Scutellar foveae more or less square, large, about 0.4 as long as scutellum, smooth, separated by a septum, the anterior margin marked, and posteriorly the margin more diffuse. Axillula moderately pubescent, their anterior and posterior margins marked. Mesopleuron (Fig. 3C) coarsely rugose and moderately pubescent; posterodorsal area less coarsely rugose and hairless.

Metanotum (Fig. 3F). Metapectal-propodeal complex. Metapleural sulcus reaching posterior margin of mesopectus at about mid-height of metapectal-propodeal

complex (Fig. 3C). Lateral propodeal carinae distinct, broad, slightly divergent. Median propodeal area with rugose sculpture, and some hairs (Fig. 3F). Nucha dorsally smooth.

Legs strong, densely pubescent; metatarsal claw with strong basal acute lobe, the secondary tooth measuring less than 1/3 of length of apical tooth (Fig. 4D).

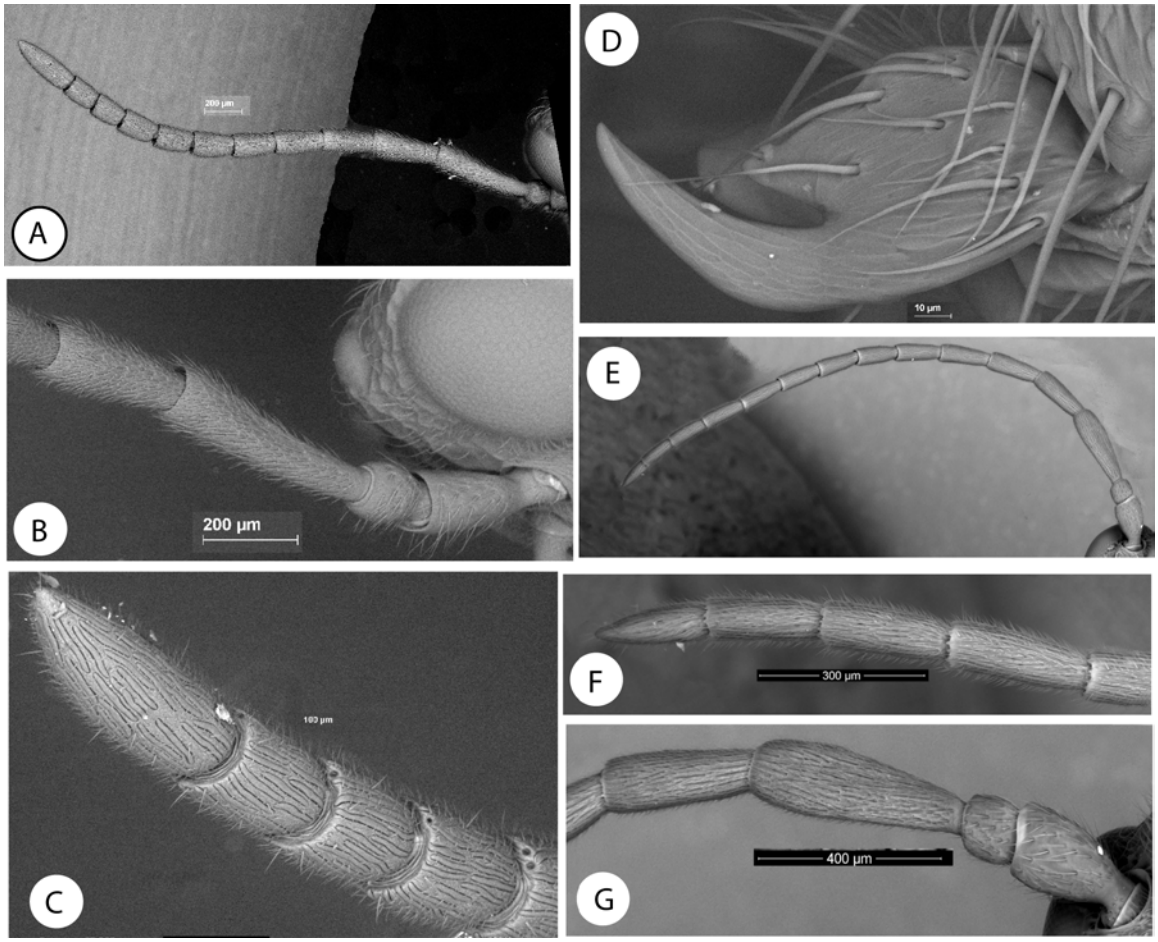

Figure 4. *Amphibolips aliciae*: (A) Female antenna. (B) Detail of basal flagellomeres. (C) Detail of last flagellomeres. (D) Metatarsal claw. (E) Male antenna. (F) Detail of last flagellomere of male antenna. (G) Detail of basal flagellomeres of male antenna.

Forewing (Fig. 7E). As long as body, veins strong and very pigmented. Radial cell 3.3 times longer than wide; open along anterior margin; areolet small, triangular, closed and distinct. Rs slightly bowed, M nearly straight, not reaching wing margin. R1 depigmented. Rs+M reaching basalis about at its mid-height. First abscissa of radius (2r) and 2r-m straight. Wing fringe on distal margin short.

Metasoma (Fig. 3E). In greater part smooth and shiny, large, as long as head and mesosoma combined, in lateral view 1.14 times longer than high. Second metasomal tergite covering about 2/3 of metasoma, posteriorly with a band of fine micropunctures hardly visible. Following tergites with micropunctures well visible. Anteroventral area

of T3 with a patch of long setae. Projecting part of hypopygial spine long; in lateral view 4 times as long as high; lateral margins of hypopygial spine with long setae but do not reach apex of spine or form an apical tuft of setae .

Male. Similar to female except as follows: Antenna with 13 flagellomeres (Fig. 4E); F1 slightly curved, flattened and expanded distally (Fig. 4G). Placodeal sensillae on F1-F13 (Figs. 4F & 4G). Relative length of antennomeres: 12:4:35:24:23:22:20:18:18:18:20:19:17:15:14. Metasoma smaller; T2 0.5 of metasoma length.

Gall. (Figs. 8D-F) Elongate, ovate or spindle-shaped, with a very short nipple at the apex (Fig. 8D). Greenish when fresh, coffee brown and very glossy when dry (Fig. 8F). The outer shell is very thin, and internally there is a single central larval cell held in place by very thin hair-like filaments (Fig. 8E). When dry the gall is very brittle, and may be easily crushed with the fingers (Fig. 8E). On average, the gall measures 2.5 mm long. Externally the gall is similar to the gall of *A. castroviejoi*. However the inner structure is different, the later being soft, juicy while the gall of *A. aliciae* is composed of radiating filaments supporting the central larval chamber.

Distribution. *A. aliciae* was found between 1000-2681 m a.s.l.at Chiriqui, Panama. Galls are rare.

Biology. Only the sexual generation of *A. aliciae* is known, inducing galls on twigs of *Quercus salicifolia* Née and likely other *Quercus* species (section Lobatae). The galls are found between December-April during the dry season in Panama. Adults emerged in January and February.

***Amphibolips salicifoliae* Medianero & Nieves-Aldrey sp. nov.**

(Figs.5, 6, 7F, 7G & 8G-H)

Type material. Holotype ♀ (Fig. 7F) (in Museo Nacional de Ciencias Naturales, Madrid, Spain, card-mounted. Cat nº 2024). PANAMA, Chiriquí, Volcan Baru 8º 47' 50 8" N, 82º 29' 35 9" W, 1800-2070m; ex gall on leaf of *Quercus salicifolia* Née (Fagaceae), gall collected 27.i.2009, insect emerged ii.09, E. Medianero leg. Paratypes: 2♀, 2♂: same data as holotype. Two paratypes in MNCN, two paratypes in Maestría en Entomología, Universidad de Panamá (MEUP).

Additionally, 1♀ of the type series was dissected for SEM observation (in MNCN).

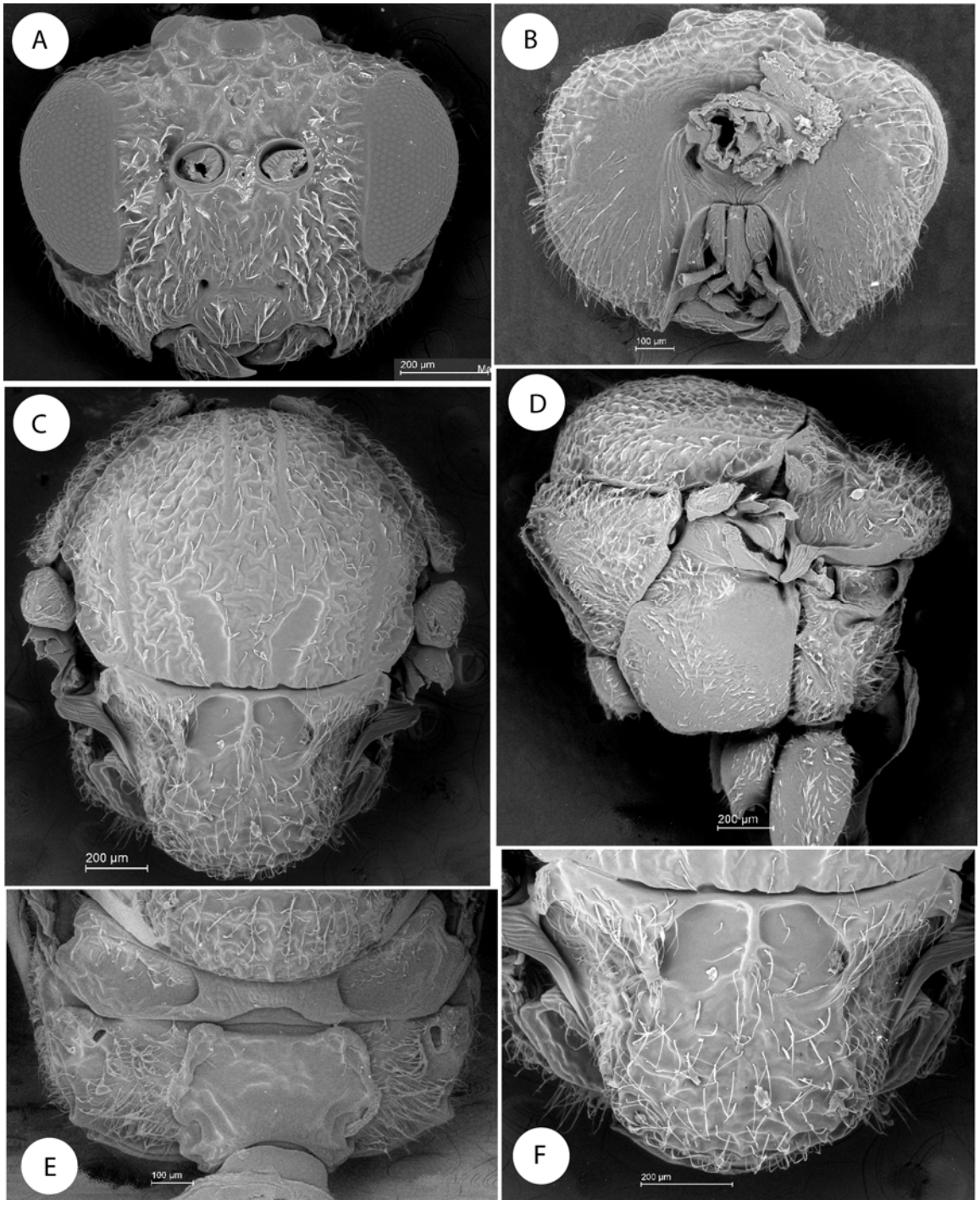

Figure 5. *Amphibolips salicifoliae*: (A) Head anterior view. (B) Head posterior view. (C) Mesosoma dorsal view. (D) Mesosoma lateral view. (E) Propodeum. (F) Scutellum dorsal view.

Etymology. Named after the hosp plant species *Quercus salicifolia.*

Diagnosis and comments. The coarsely rugose sculpture of head and mesosoma, trapezoid shape of clypeus projecting ventrally, short gula, antenna with 11 flagellomeres, with first flagellomere long, the robust and short mesosoma, with coarse rugose sculpture, the lateral carinae of propodeum slightly divergent, and the shape and setation of the hypopygial spine include the new species within the genus *Amphibolips.* Additionally, the general structure of the male, especially the 15-segmented antenna with the first flagellomere flattened and slightly expanded dorsally, and the structure of the gall, fit also well with the characters of the *Amphibolips* species. However, *A. salicifoliae* differs from all known species of *Amphibolips* by its simple metatarsal claws. From the other Panamanian *Amphibolips* species described here, *A. salicifoliae* differs, besides in claw structure, in its predominantly brown-rufous coloration, almost hyaline wings (F6-F10 at most as long as wide), its broad and smooth posterior notauli, a posterior scutellum margin that is not emarginate, metasomal tergites that are not micropunctate and by the relatively shorter projection of the hypopygial spine.

The Nearctic species *A. quercusracemaria* (Ashmead, 1881) and *A. nubilipennis* (Harris, 1841) induce similar spherical leaf galls as the galls of the new species from Panama, although the inner structure of the former is different (Melika pers. comm.). However, *A. salicifoliae* differs from *A. quercusracemaria* in at least wing coloration, the number of antennal flagellomeres and the absence of micropunctures on the metasoma. The new species is different from *A. nubilipennis* in coloration; shape of notauli, smooth scutellar foveae and absent metasomal micropunctures.

Description. Body length 3.77 mm (range 3.58-3.91; N = 3) for females; 3.15 mm (range 2.91-3.4; N = 2) for males. Head, mesosoma, metasoma and coxae of female shining brownish-rufous. Antenna and fore and middle legs, excepting coxae light yellowish hind legs yellowish brown. Forewing hyaline, with some very light infumation, veins dark brown. Male: head and mesosoma black. Metasoma black to dark brown. Mandibles, antenna and legs dark brown, excepting anterior and middle light brown tibiae and tarsi.

Female. Head, wrinkled to coarsely rugose, pubescent, in dorsal view about 2.9 times wider than long. POL 1.3 times longer than OOL, posterior ocellus separated from inner orbit of eye by 2.5 times its longest diameter. Head in anterior view more or less oval (Fig. 5A), 1.25 times wider than high. Genae not expanded behind eyes.

Vertex, frons, and occiput coarsely rugose; sculpture less strong medially on face; vertex and frons barely pubescent with sparse and shorter setae, occiput with relatively long setae. Clypeus trapezoid, 1.2 times wider than high, shining smooth, moderately pubescent, ventral margin slightly sinuate and projecting over mandibles. Anterior tentorial pits conspicuous; epistomal sulcus and clypeo-pleurostomal lines indistinct. Malar space 0.38 times as height of compound eye. Distance between antennal rim of torulus and compound eye 0.8 times its width including rim. Ocellar plate slightly raised. Head, posterior view (Fig. 5B). Gula relatively short; distance between occipital and oral foramina shorter than height of the occipital foramen. Occiput without occipital carina, with some strong transverse wrinkles. A carina dorso-lateral to occipital foramen present, curved, ventrally continuing pass posterior tentorial pits. Hypostomal sulci separated at hypostoma.

Mouthparts (Fig. 5B). Mandibles strong, exposed; with dense setae in base, right mandible with three teeth; left with two teeth. Cardo of maxilla not visible, maxillary stipes about 2.1 times longer than wide. Maxillary palp 5-, labial palp 3-segmented.

Antenna 0.4 times as long as body (Fig. 6A); with 11 flagellomeres, flagellum not broadening towards apex; with relatively long, erect setae and elongate placodeal sensilla visible only on F5–F11. Relative lengths of antennal segments: 25:15:49:31:25:26:19:17:15:15:14:13:30. Pedicel, globose, small, 0.6 as long as scape; F1 1.5 times as long as F2 (Fig. 6B). F7-F10 as long as wide or slightly transverse; F11 2.0 times longer than wide, 2.3 times as long as F10 (Fig. 6C).

Mesosoma. Coarsely rugose, 1.2 times as long as high in lateral view. Pronotum, with rugose sculpture and densely pubescent laterally. Ratio of length of pronotum medially/laterally = 0.23.

Mesonotum. Mesoscutum (Fig. 5C), moderately and uniformly pubescent, with moderately strong rugose sculpture. Notauli traceable only in posterior one third of mesoscutum length; deep, very broad, smooth and abruptly terminated. Median mesoscutal impression indistinct. Anteroadmedian signa visible. Transscutal fissure narrow. Scutellum (Fig. 5F), rounded, about 0.3 as long as mesoscutum, coarsely rugose, posterior margin not emarginate. Scutellar foveae ovoid, deep and smooth, their anterior margins forming an arc contra to transscutal fissure; posterior margins diffuse about 0.3 as long as scutellum, separated by septum. Scutellum, in lateral view, overlapping dorsellum. Mesopleuron (Fig. 5D) sculptured and setose only in medial and

basal areas, smooth and bare posterodorsally.

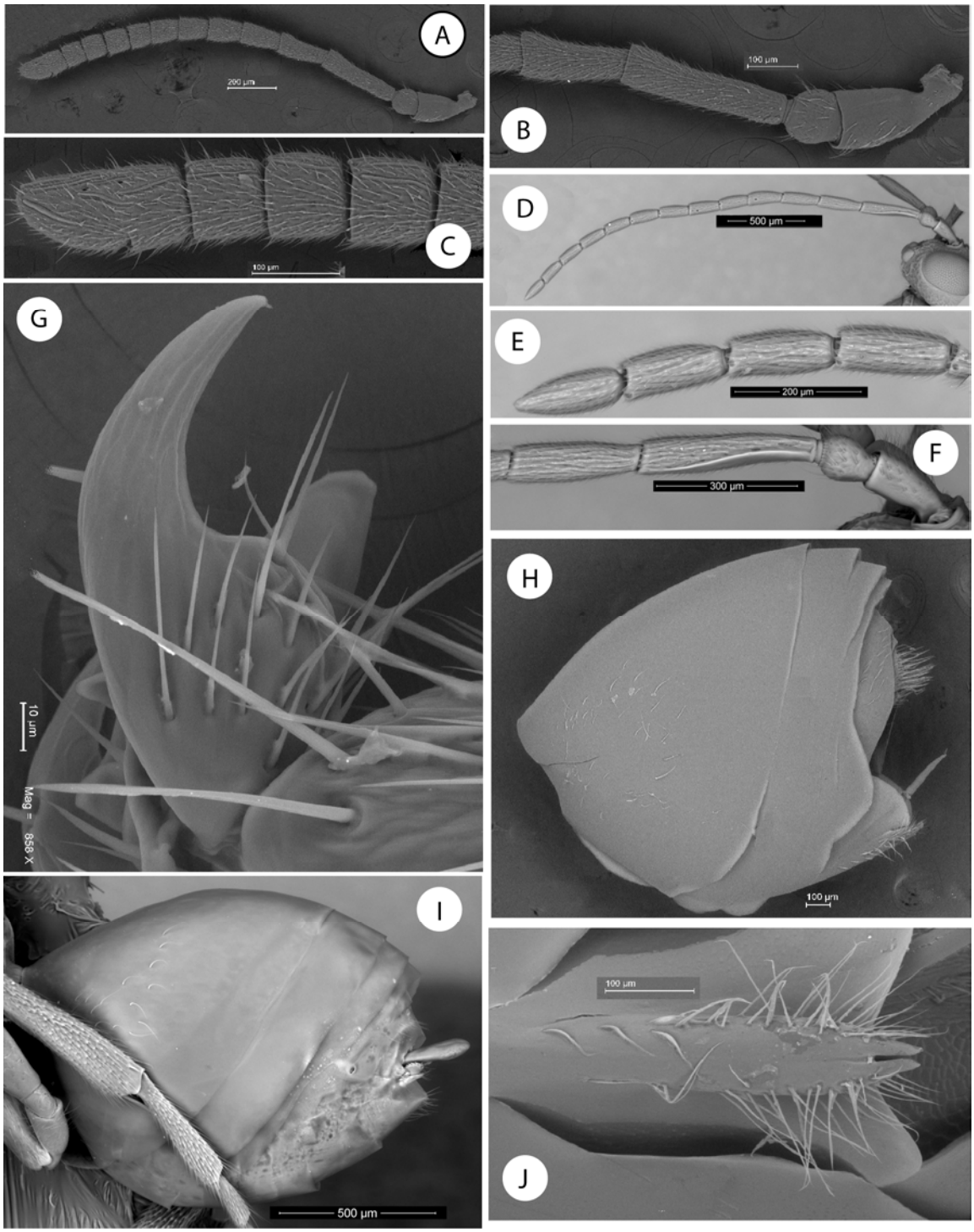

Figure 6. *Amphibolips salicifoliae*: (A) Female antenna. (B) Detail of basal flagellomeres. (C) Detail of last flagellomeres. (D) Male antenna. (E) Detail of last flagellomeres male antenna. (F) Detail of basal flagellomeres of male antenna. (G) Metatarsal claw. (H) Metasoma lateral view. (I) Matasoma male lateral view. (J) Detail of ventral spine of hypopygium.

Metanotum (Fig. 5E). Metapectal-propodeal complex. Metapleural sulcus reaching posterior margin of mesopectus at mid-height of metapectal-propodeal complex (Fig. 5D). Lateral propodeal carinae distinct, slightly divergent (Fig. 5E). Median propodeal area smooth and glabrous (Fig. 5E).

Legs. Metatarsal claws simple, without basal lobe or tooth (Fig. 6G).

Forewing (Fig. 7H). As long as body, hyaline, without conspicuous darkened spots or infuscate areas, veins strongly pigmented. Radial cell 3.6 times longer than wide; open along anterior margin; areolet small, triangular. Rs slightly bowed, M nearly straight, not reaching wing margin. Rs+M reaching basalis at its mid-height. First abscissa of radius (2r) curved, 2r-m straight. Hair fringe on apical margin short.

Metasoma (Fig. 6H). Smooth and shiny; large, as long as head and mesosoma combined; in lateral view 1.12 times as long as high. T3 covering about 2/3 of metasoma; without micropunctures; with sparsed long setae anteromedially. Projecting part of hypopygial spine, beyond attachment of lateral flap, relatively short (Fig. 6J); about 0.8 times as long as basal height of spine; in ventral view the spine is about 4 times as long as wide; lateral margins of hypopygial spine with long setae not projecting over apical end of the spine.

Male (Fig. 7G). Besides coloration, similar to female except as follows: antenna with 13 flagellomeres (Fig. 6D); F1 slightly curved and flattened (Fig. 6F). Placodeal sensillae present on all flagellomeres (Fig. 6D-F), micropores visible distally on flagellomeres 4–13. Relative length of antennomeres: 13:6:32:23:21:18:16:17:16:16:14:15:14:14:15.

Gall (Fig. 8 G-H) Regular spherical, smooth, greenish when fresh, dark brown and very glossy when dry. The outer shell is thin; internally the larval cell is central and supported by thin hair-like radiating filaments (Fig. 8 H). When dry the gall is very brittle, and may be easily crushed with the fingers. Diameter of the gall measures 30 mm on average.

Distribution. *A. salicifoliae* was found between 1870-2680 m a.s.l. at the single site of Volcan Baru, Panama. In comparison with *A. castroviejoi* is a rare species.

Biology. Only the sexual generation of *A. salicifoliae* is known, inducing galls on the underside of *Quercus salicifolia* leaves. Galls are found between January-April, during the dry season, and the insects emerge in the same season. This species displays a remarkable sexual dimorphism in coloration.

Key to *Amphibolips* species of Panama

1. Metatarsal claw with large acute basal lobe or secondary tooth (Figs. 2D, 4D); sculpture of mesoscutum and mesopleuron strongly and coarsely rugose; notauli complete or slightly faint in anterior one third of mesoscutum, crossed by transversal sculpture (Figs. 1C, 3D); median area of propodeum sculptured and pubescent (Figs. 1F, 3F). Metasomal tergites with micropuntures (Figs. 2H, 3E). Forewing strongly infuscate or with smoky area in radial cell (Figs. 7C, 7G). Galls globose or spindle-shaped on twigs (Figs. 8A, 8D)…….**2**

- Metatarsal claws simple (Fig. 6G), without basal lobe or tooth; sculpture of mesoscutum and mesopleuron weaker; notauli traceable only in posterior one third, deep, broad and smooth (Fig. 5C); median propodeal area smooth and glabrous (Fig. 5E). Metasomal tergites without micropunctures (Fig. 6H). Forewing almost hyaline, only slightly smoked (Fig. 7H). Galls spherical, on leaves (Fig. 8G). ……...***A. salicifoliae***

2. Notauli complete, slightly faint along coarse surface of anterior one third of mesoscutum; posteriorly narrow and slightly convergent (Fig. 1C); scutellum deeply emarginate at the posterior margin (Fig. 1C); scutellar foveae ellipsoid, with well defined posterior margins. Posterior 1/3 of T2 with a band of well-visible micropunctures (Fig. 2H); forewing very heavily and entirely smoky, except clear and wide band extending across wing from radial cell to ventral margin (Fig. 7C). Gall globose, oak apple type, with inner structure soft, juicy (Figs. 8B, 8C)…..……...***Amphibolips castroviejoi***

   Notauli complete and broad; posteriorly broader and strongly convergent (Fig. 3D); scutellum only slightly emarginate at the posterior margin; scutellar foveae relatively larger, with straight anterior margins and faint posterior margins (Fig. 3D). Posterior 1/3 of T2 with a band of hardly visible micropunctures; forewing only slightly smoked, with a large brown patch at the base of the radial cell (Fig. 7E). Gall spindle-shaped (Fig. 8 D-E)…. ……***Amphibolips aliciae***.

Discussion

The new species described here represent advancement in knowledge of the taxonomy, biology and distribution of the genus *Amphibolips*. Regarding the morphological diagnosis of *Amphibolips*, the use of few and problematic characters (e.g., the metatarsal claw) for the separation of Cynipini genera is well documented in the literature on the group (Nieves-Aldrey 1992, 2001), especially with reference to some Nearctic genera of that tribe (Melika & Abramhason 2002; Liljeblad *et al*. 2008, and references cited therein). The genus *Amphibolips*, defined, among other characteristics, by its toothed metatarsal claws, should be now included among the genus that are variable for this character because the new species, *Amphibolips salicifoliae*, has simple metatarsal claws without a basal lobe or tooth. However, the new species show all the clear diagnostic morphological characters of *Amphibolips*. Their galls are of the typical form shared by all the species of this genus.

The discovery of the presence of *Amphibolips* in Panama represents the southernmost known distribution of this genus in America, confirming that it is well represented in Central America and the Neotropical Region. We predict that the genus could be revealed to be even more species-rich in this biogeographical region after new collections are made in neighboring countries in Central America and South America; for example, the presence of Cynipidae on *Quercus humboldtii* has been recently documented in Colombia (Nieves-Aldrey, 2005).

The species of *Amphibolips* are only found on *Quercus* species in the section Lobatae, a host plant association reinforced by the three new species from Panama, which induce galls on *Q. salicifolia*. This pattern is also present in other undescribed species collected in Mexico (E. Pascual, pers. comm.).

The inquiline and parasitoid community associated with the galls.

The galls of the new species of *Amphibolips* here described host an interesting community of cynipid inquilines and chalcidoid parasitoids. One undescribed species of *Synergus* was reared from galls of *Amphibolips castroviejoi* and *A. aliciae*, while another undescribed species was reared from the galls of *A. salicifoliae*. A striking torymid species (*Torymus* Dalman: Torymidae) was reared from the galls of *A. castroviejoi*. These species are being studied and results will be published elsewhere.

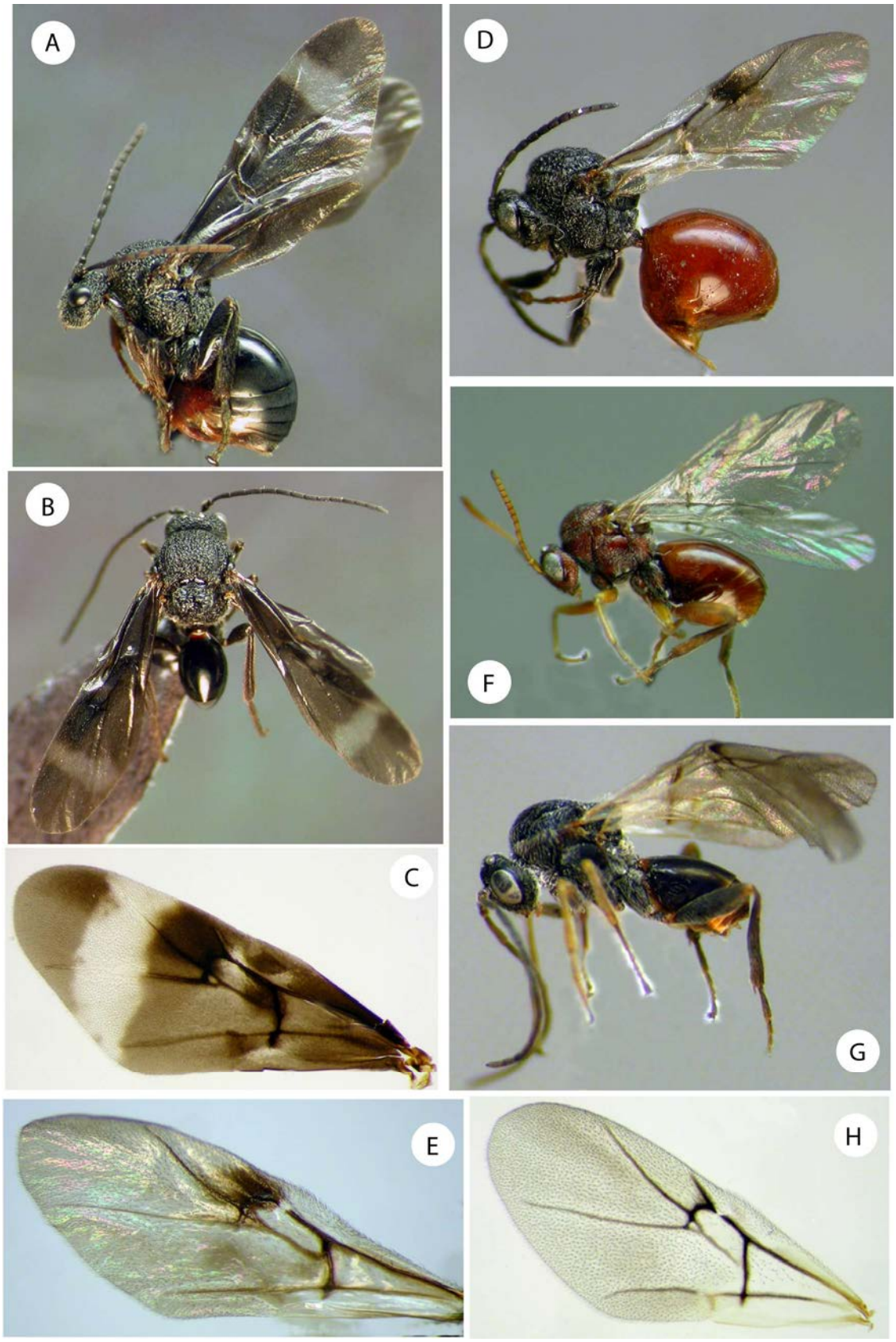

Figure 7. Habitus and forewings of *Amphibolips* species: (A) *Amphibolips castroviejoi*, female (B) *A.castroviejoi*, male (C) forewing of female. (D) *Amphibolips aliciae.* (E) forewing of female. (F) *A. salicifoliae*, female. (G) *A. salicifoliae*, male. (H) forewing of female.

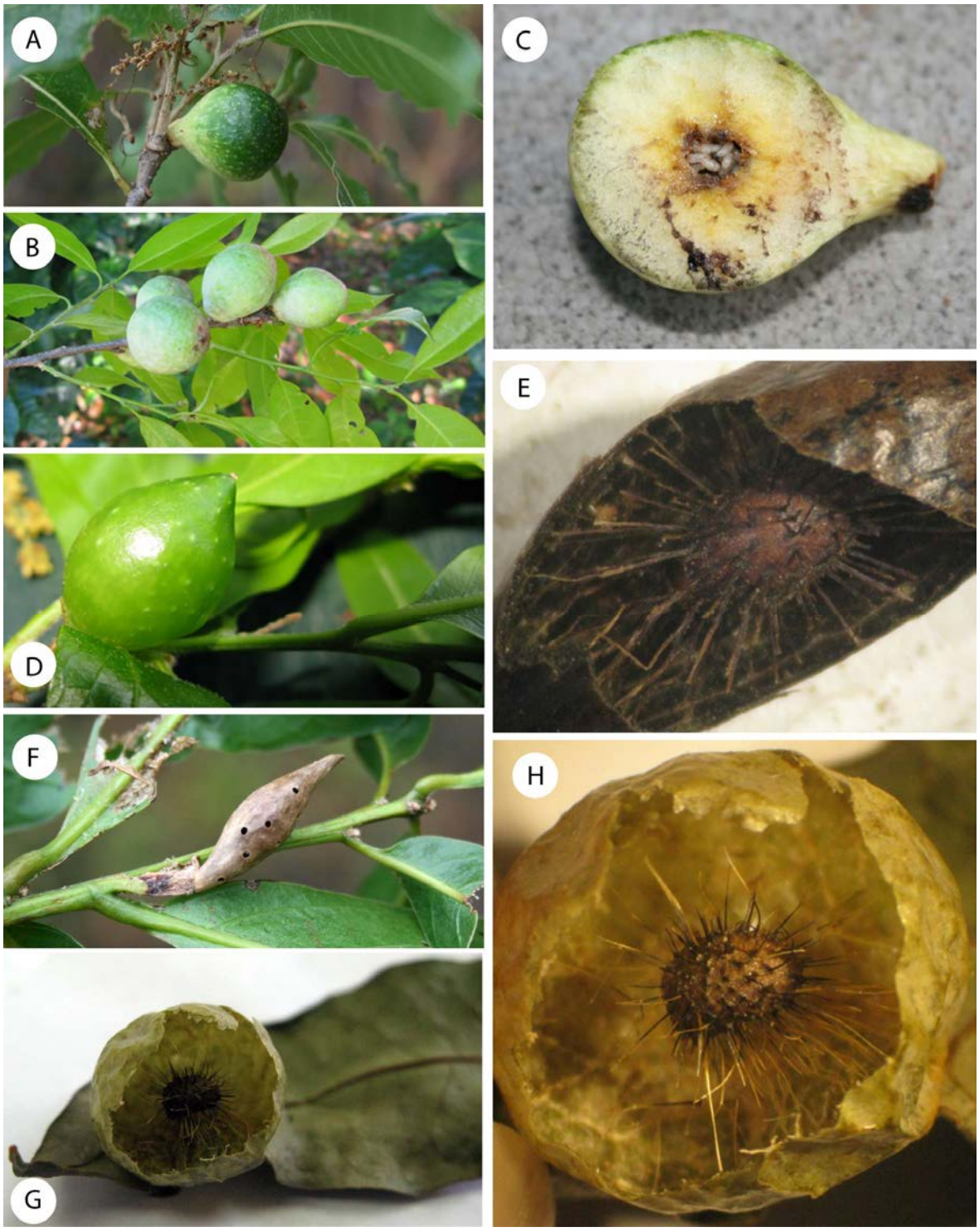

Figure 8. Galls of *Amphibolips* species from Panama: (A) Immature gall of *Amphibolips castroviejoi*. (B) Group of mature galls. (C) Section of a gall showing the central cell with the larvae of a gregarious parasitoid. (D) Mature gall of *Amphibolips aliciae*. (E) Section of a dry gall. (F) An old *A. aliciae* gall showing the exit holes of parasitoid species. (G) *Amphibolips salicifoliae* leaf gall. (H) Section of a mature gall.

Acknowledgements

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2.2-Descripción de la primera especie neotropical de *Bassettia* Ashmead de Panamá (Hymenoptera: Cynipidae: Cynipini[3])

RESUMEN

Se describe una nueva especie de *Bassettia* Ashmead 1887*, Bassettia caulicola* (Hymenoptera: Cynipidae: Cynipini), de Panamá. La nueva especie induce agallas en los tallos de *Quercus bumelioides* Liebm. (Fagaceae secc. *Quercus*). Se aportan los caracteres diagnósticos de la nueva especie, su distribución y su biología. La nueva especies es incluida en la clave de identificación de la especies de *Bassettia* del Neártico. Se amplían los datos diagnósticos morfológicos del género *Bassettia* así como se comenta el primer registro de este género en la región neotropical.

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Description of the first Neotropical species of *Bassettia* Ashmead (Hymenoptera: Cynipidae: Cynipini) from Panama

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ABSTRACT

A new species of *Bassettia* Ashmead 1887*, Bassettia caulicola* (Hymenoptera: Cynipidae: Cynipini), from Panama is described. The new species induces galls on the stems of *Quercus bumelioides* Liebm. (Fagaceae sect. *Quercus*). The diagnostic characteristics, distribution data, and biology of the new species are given. The new species is included in the existing key for the identification of the Nearctic species of *Bassettia*. The morphological diagnosis of *Bassettia* and the first record of this genus in the Neotropical region are noted.

Key words: Cynipidae, oak gall wasps, *Bassettia, Quercus,* Panama

Introduction

Bassettia Ashmead is a small genus of oak gall wasps (Cynipidae: Cynipini) from North America (Weld, 1952). Species of this genus have been collected in several states of the USA, including Arizona, California, Colorado, Florida, Georgia, Missouri, New Mexico, Virginia and Oregon (Kinsey, 1922; Melika & Abrahamson, 2007). Morphologically and biologically, *Bassettia* is closely related to the genera *Plagiotrochus* Mayr, 1881; *Callirhytis* Foerster, 1869; and *Loxaulus* Mayr, 1881 (Melika & Abrahamson, 2002). Currently, the genus *Bassettia* includes eight species (Melika & Abrahamson, 2007) that induce galls on white oaks. The species of this genus induce cryptic stem galls that develop under the bark of twigs in the form of

elongated larval cells that usually do not cause swelling. The presence of the cryptic galls is usually evidenced by emergence holes of the adult insects on the twig surface. The known sexual generations induce small oval swellings on leaves (Kinsey, 1922; Melika & Abrahamson, 2007).

Since Ashmead (1887) proposed the genus *Bassettia*, new characters have been added for a better diagnosis of the genus (see Weld, 1921). Although Melika & Abrahamson (2007) have reviewed and redescribed the genus *Bassettia* recently, the taxonomic status of this genus is still problematic given the difficulty in finding phylogenetically informative or reliable characters that accurately define the genus and its limits with the closely related genera *Loxaulus*, *Plagiotrochus* and *Callirhytis.*

This paper is the first report of the genus *Bassettia* in Central America and includes a description of one new species from Panama. For the first time in *Bassettia,* the description of the morphological characters of a species is based on scanning electron microscopy, allowing the discussion of some new diagnostic characters of the genus.

Material and methods

Study material. The insects studied were reared from galls collected from *Quercus bumelioides* Liebm. The adult insects emerged from the galls in rearing cages under laboratory conditions.

Specimen preparation. For observation under a scanning electron microscope (SEM), adult cynipids were observed without dissection using SEM at low vacuum, without coating. Micrographs were taken using an FEI QUANTA 200 microscope (low vacuum technique). Images of adult habitus, forewings and gall dissections were taken using a NIKON Coolpix 4500 digital camera attached to a Wild MZ8 stereo microscope. Measurements were made using a calibrated micrometer scale attached to an ocular of the light microscope. The terminology of morphological structures and abbreviations follow Ronquist & Nordlander (1989), Ronquist (1995), Nieves-Aldrey (2001) and Liljeblad *et al.* (2008).

Results

***Bassettia caulicola* Medianero & Nieves-Aldrey sp. nov.**

(Figs. 1, 2 & 3)

Type material. Holotype ♀ (Fig. 3A) (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. Cat. nº 2110). PANAMA, Chiriquí, Volcan Baru, 8º 46' 36 8" N, 82º 31' 39 3" W, 2870 m; ex gall on stem of *Quercus bumelioides* Liebm. (Fagaceae), gall collected 22.xii.2008, insect emerged i.09, E. Medianero leg.

Etymology. Named after the stem cryptic gall of this species.

Diagnosis and comments. The form of the head in frontal view, broadened genae behind eyes, the malar space without a sulcus, scape and pedicel broad and strongly flattened, elongated body, mesosoma flattened dorso-ventrally, mesoscutum transversely rugose, propodeum with two parallel lateral propodeal carinae and a median incomplete longitudinal carina, the tarsal claws simple, and third abdominal tergum with a ring of white setae at base, interrupted dorsally, includes the new species within the genus *Bassettia.* Additionally, the structure of the gall also agrees well with the characters of the *Bassettia* species. However, *B. caulicola* differs from all known species of *Bassettia* by its face with radiating striae from clypeus, reaching ventral margin of the eye and toruli and extending into the area between toruli and eye. Additionally, *B. caulicola* differs from all known species of *Bassettia* by the 15 segmented antenna; the relatively shorter third abdominal tergum, not reaching half the length of the metasoma and by the shorter projection of the hypopygial spine.

The Nearctic species *B. tenuana* (Weld, 1921) and *B. virginiana* (Melika & Abrahamson, 2007) resemble in color the new species from Panama. However, *B. caulicola* differs from *B. tenuana* and *B. virginiana* at least in the number of antennal segments, the relatively longer projection of the hypopygial spine and the face with radiating striae from clypeus.

Description. Body length (measured from the anterior margin of the head to the posterior margin of the metasoma) 3.5 mm (N = 1) for females. Head and mesosoma of female black. Metasoma chestnut reddish, with one black spot in the anterodorsal area of T3 covering middle tergite. Mandibles, scape, pedicel, F1 y F2 of antenna,

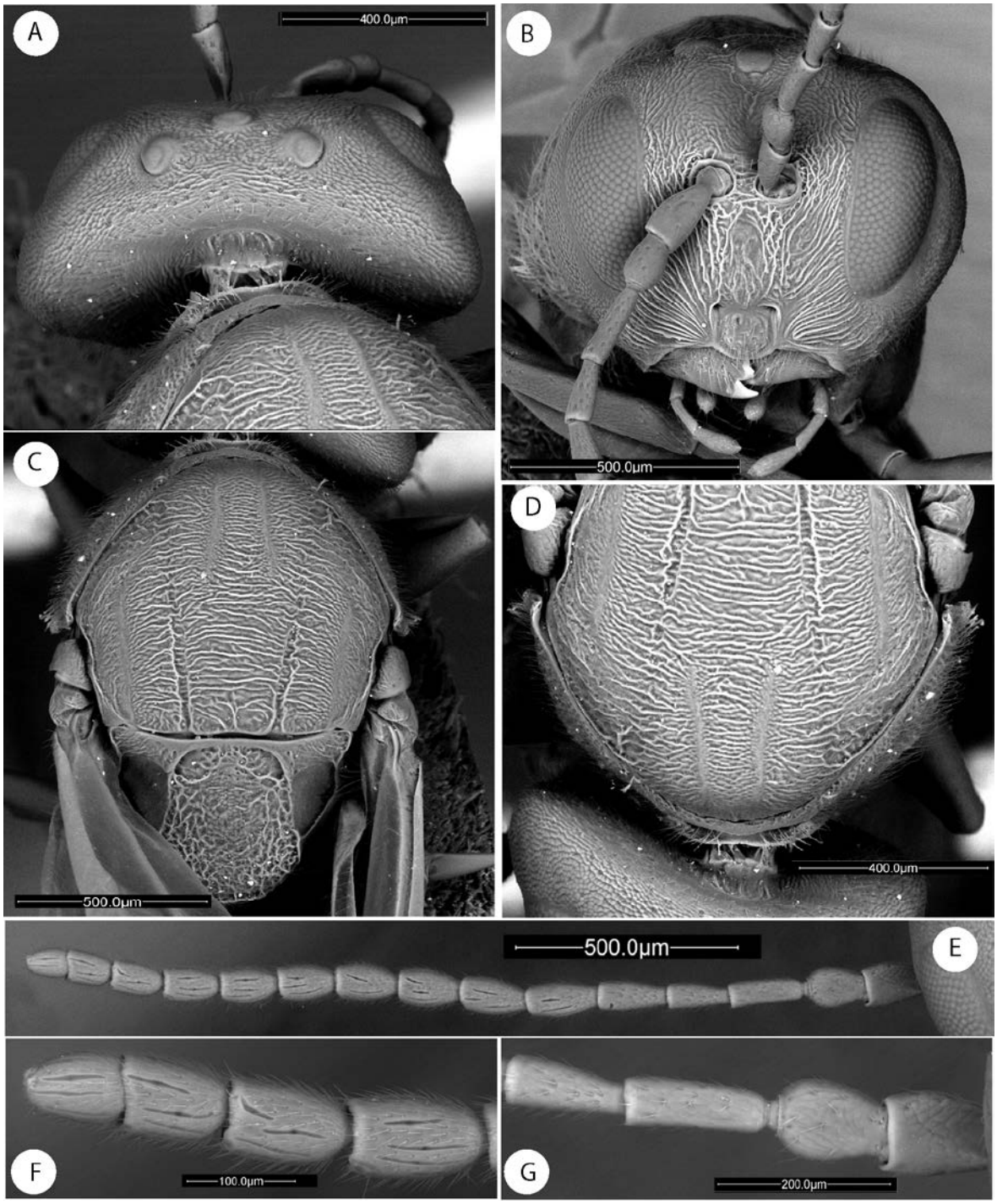

Figure 1. *Bassettia caulicola*: (A) Head dorsal view. (B) Head anterior view. (C) Mesosoma dorsal view. (D) Pronotum antero-dorsal view. (E) Female antenna. (F) Detail of last flagellomeres. (G) Detail of basal flagellomeres.

trochanter, apical parts of the femora, tibiae and tarsi of fore and middle legs light brown. Coxae, femora and F3 – F13 of antenna dark brown to black. Forewing hyaline and veins light brown.

Female. Head in dorsal view approximately 2.5 times wider than long, as wide as mesosoma (Fig. 1A). POL 1.6 times longer than OOL, posterior ocellus separated from inner orbit of eye by 1.5 times its longest diameter. Head in anterior view (Fig. 1B) rounded, 1.1 times wider than high, genae strongly expanded behind eyes. Vertex, frons, and genae, alutaceous and bare. Occiput finely alutaceous, moderately pubescent with short white setae. Face with radiating striae from clypeus, reaching ventral margin of eye and toruli and extending into area between toruli and eye; the striae are present laterally, being more diffuse medially on the face; they are stronger and branched close to the ventral margin of the toruli. Clypeus square, smooth, moderately pubescent, the ventral margin slightly projecting over mandibles. Anterior tentorial pits, epistomal sulcus and clypeo-pleurostomal lines visible. Malar space 0.3 times as long as height of compound eye. Toruli situated to mid-height of compound eye; distance between antennal rim and compound eye 1.2 times width of antennal socket including rim. Ocellar plate not raised. Occipital carina absent.

Mouthparts (Fig. 1B), mandibles strong, exposed; with dense white setae in base, right mandible with three teeth; left with two teeth.

Antenna (Figs. 1E-G) of moderate length, as long as 1/2 body length; with 15 segments; flagellum not broadening towards apex; with relatively shorter, erect setae, and elongate placodeal sensilla visible on F4-F13 (Fig. 1F). Relative lengths of antennal segments: 15:13:19:15:17:17:16:15:15:14:13:13:13:11:10. Pedicel (Fig. 1G), broad and flattened, 1.5 as long as wide and 0.8 as long as scape; F1 1.3 times as long as F2, slightly flattened ventrally. F6-F13 longer than wide, F13 1.4 times longer than wide, as long as F12 (Fig. 1F). Placodeal sensillae on F4-F13 disposed in one row of 2-3 sensillae in each flagellomere.

Mesosoma in lateral view 1.3 times longer than high (Fig. 2A). Pronotum, pubescent; lateral surface of pronotum weakly coriaceous rugose; ratio of length of pronotum medially/laterally = 0.27; pronotal plate indistinct dorsally (Fig. 1D).

Mesonotum (Fig. 1C). Mesoscutum transversely rugose and weakly pubescent. Notauli percurrent posterior and medially, scarcely traceable in anterior one third; not quite convergent posteriorly, crossed by the transversal striate sculpture; median mesoscutal impression indistinct, lost in the rugose sculpture. Anteroadmedian signa clearly visible. Transscutal fissure narrow. Scutellum (Fig. 1C) in dorsal view longer

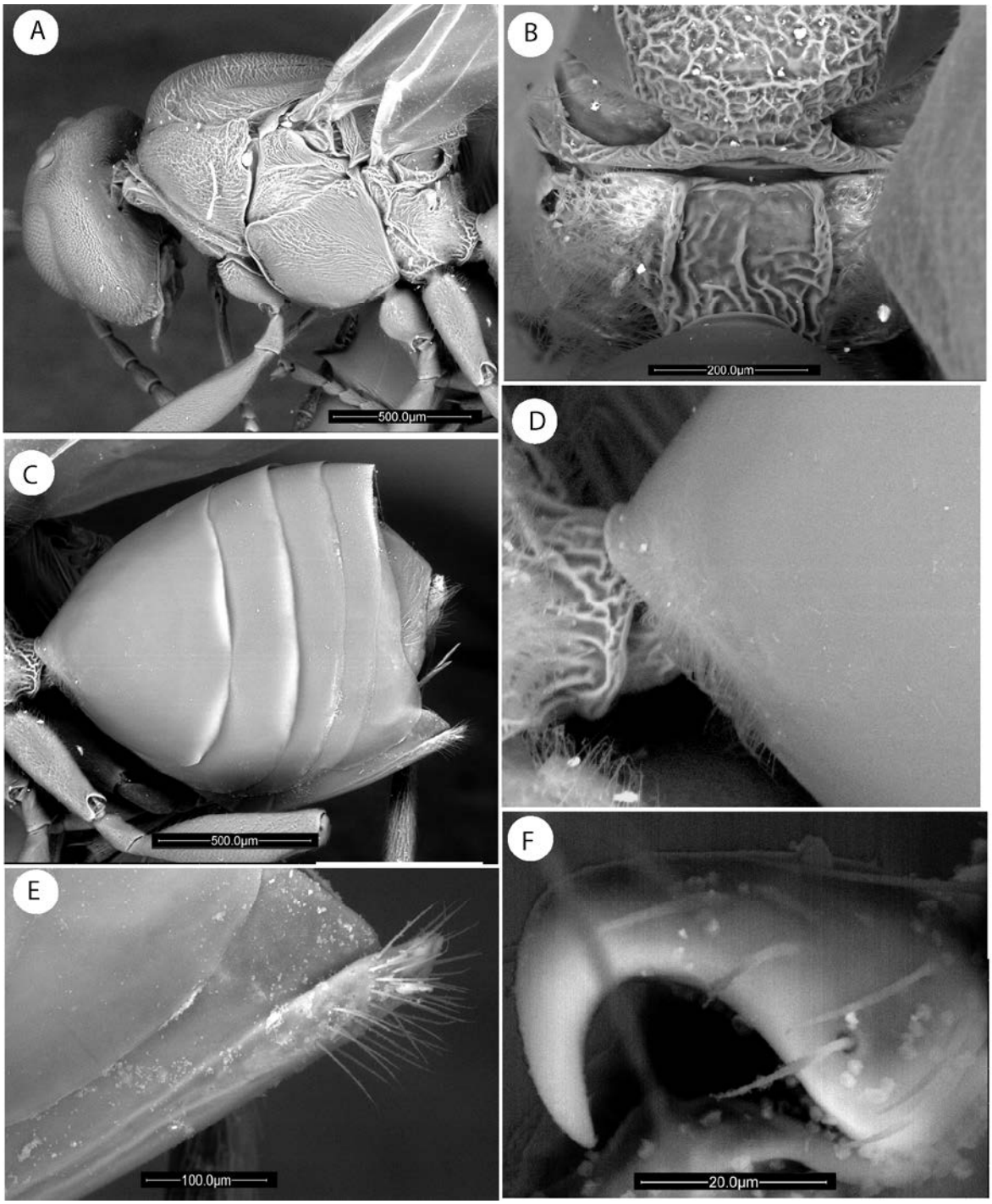

Figure 2. *Bassettia caulicola*: (A) Mesosoma lateral view. (B) Propodeum. (C) Metasoma lateral view. (D) Detail ring of setae at base of third abdominal tergum. (E) Detail of ventral spine of hypopygium. (F) Metatarsal claw.

than wide, approximately 0.5 times as long as mesoscutum, uniformly reticulate-rugose, in lateral view only slightly extended posteriorly over the dorsellum. Scutellar foveae ellipsoidal, small; approximately 1/6 as long as scutellum, not deep, the inner margins scarcely distinct, lost in the rugose sculpture; their posterior margins weakly marked.

Mesopleuron with some transversal striae in the medial area and alutaceous sculpture in the interspaces, the sculpture also present although weaker on dorsal and ventral areas of mesopleuron (Fig. 2A).

Metanotum (Fig. 2B). Metapectal-propodeal complex. Metapleural sulcus meeting posterior margin of mesopectus at mid-height of metapectal-propodeal complex (Fig. 2A). Lateral propodeal carinae distinct, strong, subparallel, (Fig. 2B); median propodeal area narrow, with a median longitudinal carina incomplete dorsally and bare, sides of propodeum outward of central area densely pubescent with relatively long white setae. Nucha with some longitudinal rugae.

Legs moderately pubescent; femora and tibiae slender; metatarsal claws simple, with a strongly bent apical tooth and without a basal lobe or tooth (Fig. 2F).

Forewing (Fig. 3B) as long as body, veins strongly pigmented. Radial cell 3.5 times as long as wide; open along anterior margin; areolet, triangular. First abscissa of radius not bumped, second abscissa of radius slightly bent, apically not reaching margin of wing. M short, nearly straight, only reaching half wing. Rs+M reaching basalis at its mid-height. A short hair fringe on apical margin of wing.

Metasoma (Fig. 2C) 0.8 times as long as head and mesosoma combined, in lateral view 1.2 times longer than high. Third abdominal tergum covering one third of metasoma, with a ring of white setae laterally at its base, interrupted dorsally (Fig. 2D); subsequent tergites smooth and bare. Projecting part of the hypopygial spine short (Fig. 2E); barely 1.1 times as long as wide in ventral view; lateral margins of the hypopygial spine with setae reaching the apex of spine, but not forming an apical hair patch.

Gall (Fig. 3 C & D). Stem galls develop under the bark of twigs of *Q. bumelioides* in the form of elongated larval cells that usually do not cause swellings (Fig. 3D). The only evidence of galling is the presence of typical adult emergence holes (Fig. 3C). The galls containing fully developed adults are found in December, at the beginning the dry season in Panama. The studied insects emerged in January.

Distribution. Based on our data, *B. caulicola* is found between 2870-3100 m at Chiriqui, Panama, around the upper limit of growing of *Quercus* species in Panama.

Biology. Only the asexual generation is known, inducing galls on *Quercus bumelioides* Liebm. (= *Q. copeyensis*).

In the key for the identification of the Nearctic species of *Bassettia* (Melika & Abrahamson 2007), the new species goes to couplet 6 and can then be distinguished as follows:

● Radiating striae from clypeus present, reaching the ventral margin of the eye and toruli. Antenna with 15 segments. Projection of hypopygial spine approximately as long as wide. ..... ***B. caulicola*** *sp*. nov.

● Radiating striae from clypeus completely absent. Antennae with 14 segments. Projection of the hypopygial spine clearly longer than wide**.....**

Nearctic species of *Bassettia* (*B. gemmae, B. ligni, B. floridana, B. pallida, B. virginiana, B. weldi, B. tenuana*..)

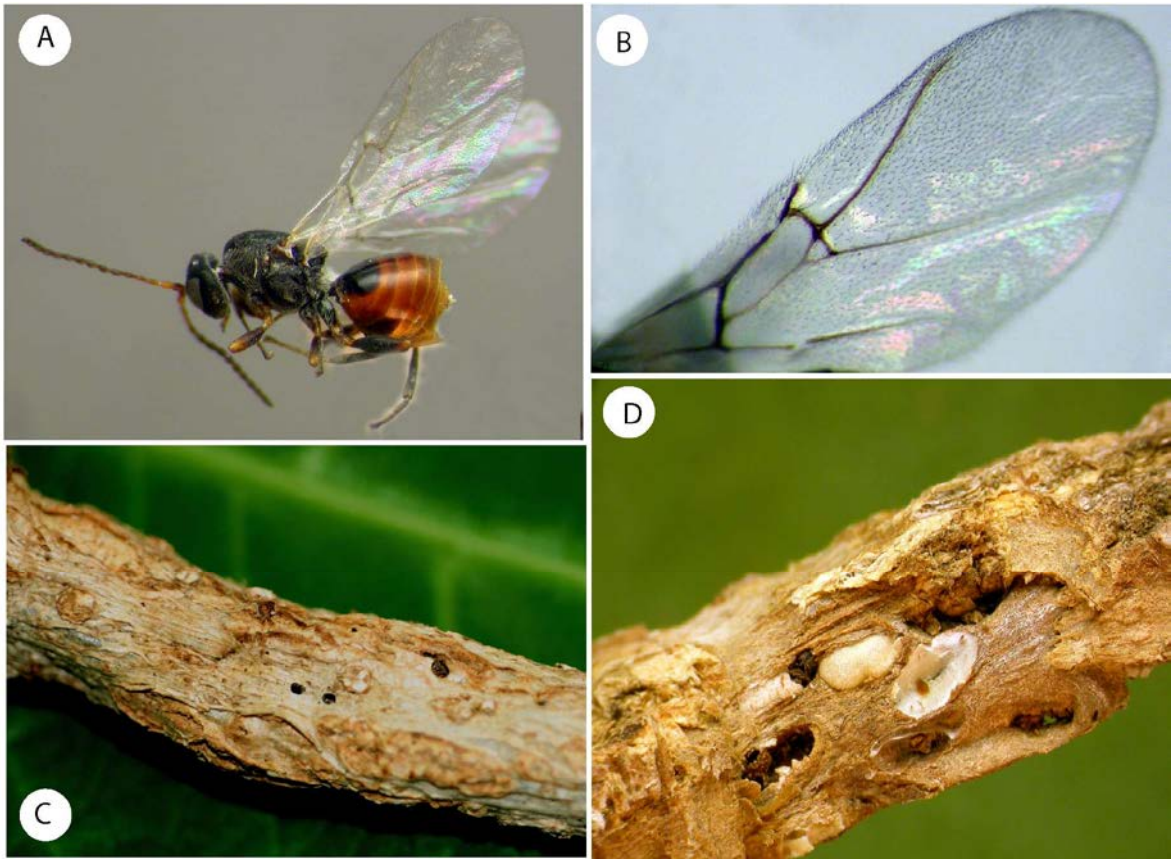

Figure 3. *Bassettia caulicola*: (A) Habitus, female. (B) Forewing of female. (C) Mature gall, showing the adult emergence holes. (D). Section of a gall showing the larval cells.

Discussion

The study of this new species from Panama created some doubts in us regarding its correct generic classification within *Bassettia* given the presence of some character states that do not fit with the diagnosis of this genus in the recent revision of Melika & Abrahamson (2007), namely the presence of facial radiating striae, the number of antennal segments and the relative length of the hypopygial spine. However, in all the remaining characters the new species fits well in *Bassettia,* and we prefer to be conservative in deciding its generic placement. If our classification is correct, the taxonomic limits of *Bassettia* should be enlarged to include the new diagnostic characters. Within the tribe Cynipini, the new species is also closely similar in many characters to species of the genera *Callirhytis* Foerster and *Plagiotrochus* Mayr, mainly for the presence of a transversely striated mesoscutum and facial striae. However, the species of *Plagiotrochus*, in addition to its different geographic distribution, host plant data and biology, have a different mesopleural sculpture and a different conformation of the propodeum, with lateral propodeal carinea bowed or angulated (these are subparallel in *Bassettia*). With regard to its affinities with the genus *Callirhytis*, the new species shares some characters with this genus, such as the presence of radiating striae on the face, subparallel lateral propodeal carina, wrinkled mesoscutum and a short hypopygial spine. However, the absence of a malar sulcus, the presence of a median propodeal carina and the characters of the forewings exclude the new species from the genus *Callirhytis*.

A final, closely related genus to *Bassettia* is *Loxaulus,* of which we describe two new species from Panama (Medianero *et al*., in prep.). The species of *Loxaulus* share with *Bassettia* a similar biology and galls, as well as a closely similar morphology. However, the species of the two genera can be distinguished by the presence of a conspicuous malar sulcus and a different forewing venation in the *Loxaulus* species. The limits of these closely allied genera are imprecise as demonstrated by their taxonomic and nomenclatorial instability. More taxonomical, revisional and phylogenetic work is clearly needed to clarify the issue. Hopefully, recent morphological phylogenetic analysis (Liljeblad *et al*., 2008) and other ongoing molecular phylogenetic studies will throw light on the phylogenetic relationships of the Cynipini and allow new, more natural and stable generic classifications.

The discovery of *Bassettia* in Panama represents the southernmost known distribution of this genus in America, confirming that it is represented in Central America and the Neotropical Region. We predict that the genus could be demonstrated to be even more species-rich in this biogeographical region after new samplings are made in Mexico and Central America.

Acknowledgements

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2.3-Primera cita del género *Disholcaspis* Dalla Torre & Kieffer (Hymenoptera: Cynipidae: Cynipini) en el Neotrópico, con la descripción de dos nuevas especies de Panamá[4].

Resumen

Dos nuevas especies de *Disholcaspis* Dalla Torre & Kieffer 1910, *Disholcaspis bettyannae* y *D. bisethiae* (Hymenoptera: Cynipidae: Cynipini) son descritas de Panamá. Las dos nuevas especies inducen agallas en *Quercus bumelioides* Liebm. y *Q. lancifolia* Schledl & Cham. (Fagaceae, secc. Quercus, robles blancos). Se presentan los caracteres diagnósticos incluyendo una clave de identificación, asi como la descripción de las agallas, su distribución, y la información biológica de las nuevas especies. Las nuevas especies representan el primer registro del género *Disholcaspis* del Neotropico.

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First record of the genus *Disholcaspis* Dalla Torre & Kieffer (Hymenoptera: Cynipidae: Cynipini) in the Neotropics, with description of two new species from Panama

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Abstract

Two new species of *Disholcaspis* Dalla Torre & Kieffer 1910, *Disholcaspis bettyannae and D. bisethiae* (Hymenoptera: Cynipidae: Cynipini) are described from Panama. The two new species induce galls on *Quercus bumelioides* Liebm. and *Q. lancifolia* Schledl & Cham. (Fagaceae, sect. Quercus, White Oaks). Diagnostic characters, gall descriptions, distribution, and biological data of the new species are given. The new species represent the first records of the genus *Disholcaspis* from the Neotropical region.

Key words: Cynipidae, oak gall wasps, *Quercus*, Chiriqui, Panama

Introduction

Disholcaspis Dalla Torre & Kieffer (=*Holcaspis* Mayr) is a genus of oak gall wasps (Cynipidae: Cynipini) recorded as being confined to the Nearctic (Dalla Torre & Kieffer 1910; Weld 1952). To date, 52 species are known (Liljeblad *et al.* 2008): 41 from the United States and Canada, and 11 from Mexico (Burks 1979; Kinsey 1937, 1938; Melika & Abrahamson 2002). Although the genus was also mentioned as present in Costa Rica (Central America) by Pujade-Villar & Hanson (2006), no species have

been described or recorded to date from the Neotropical region.

The nomenclature and classification within this genus has been unstable; Burks (1979) cited 38 species and one variety from the United States & Canada. Dailey & Menke (1980) transferred *D. truckeensis* Ashmead to *Andricus* Hartig. Melika & Abrahamson (2002), transferred three *Andricus* species to *Disholcaspis: A. lasius* Ashmead; *A. reniformis* McCracken & Egbert; and *A. spectabilis* Kinsey, but this taxonomic act was later considered erroneous (Pujade-Villar *et al.* 2010). Additionally, the following species from the western United States: *D. chrysolepidis* Beutenmüller; *D. canescens* Bassett; *D. conalis* Weld; *D. corallina* Bassett; *D. plumbella* Kinsey; *D. sulcata* Ashmead and *D. washingtonensis* Gillette differ in some aspects of the diagnosis typical of the genus *Disholcaspis* (Weld 1952), and according to Melika & Abrahamson (2002), eventually could be transferred to other genera. More recently, one species described from Mexico, *D. lapiei* Kieffer, has been transferred to the new genus *Kinseyella* Pujade-Villar & Melika (Pujade-Villar *et al.* 2010).

All the known species of *Disholcaspis* induce galls on white oaks (Fagaceae, section *Quercus*) (Weld 1952; Liljeblad *et al.* 2008). Whereas the adults of *Disholcaspis* are morphologically quite uniform and hardly differentiated (Weld 1952) (many species are based in differences of coloration), the galls of each species are usually quite distinctive (Weld 1952, 1957). The asexual generation of the species of *Disholcaspis* induces detachable galls, single or clustering in groups, on the twigs, roots and buds of various species of white oaks, whereas the sexual generation emerges from small, thin-walled bud galls (Weld 1952; Evans 1972; Melika & Abrahamson 2002).

The adults of the asexual generation of the species of *Disholcaspis* are recognized as follows (see also Beutenmüller 1909; Melika & Abrahamson 2002): robust individuals, antenna 13-14 segmented, with scape stout, and very short and stout pedicel, flagellomeres F1-F6 long and slender, gradually decreasing in length, last flagellomeres short and somewhat thickened; without a malar sulcus, mesonotum with notauli incomplete, faintly anteriorly; scutellum rounded, convex; scutellar foveae not well differentiated, indistinctly separated medially, usually forming a shallow transverse depression, sometimes virtually absent; in profile, the scutellum is prolonged posteriorly far beyond propodeum; lateral propodeal carinae bowed or angulated, median propodeal area with some carinae or strong rugae; second metasomal tergum conspicuously pubescent at its base; metatarsal claws with a secondary basal tooth; projecting part of

hypopygial spine short to moderately long, maximally 2.0 – 3.5 times as long as broad, hypopygial setae not forming an apical tuff. The adults of the sexual generation can be distinguished by the head lunate from above, scarcely broadened behind eyes, antenna of 14 segments, thorax smooth and shining, with conspicuous microreticulation anteriorly and laterally, notauli faint anteriorly, scutellum elongate, gradually and very slightly depressed towards the transscutal articulation, scutellar foveae indistinctly defined, mesopleuron bare and shiny; abdomen slightly longer than thorax, second metasomal tergite finely punctuate and pubescent, ventral spine short, seldom twice as long as wide (Evans 1972; Melika & Abrahamson 2002).

Morphologically and biologically, *Disholcaspis* share some similarities with *Aphelonyx*, a Palaearctic genus, represented by only three species (Melika *et al*. 2010). The type species of both genera, *A. cerricola* and *D. quercusglobulus,* were recovered in a strongly supported clade in the recent phylogenetic analysis by Liljeblad *et al.* (2008). In the framework of a field study of the oak gall wasps (Cynipidae) of Panama (see also Medianero & Nieves-Aldrey 2010; Nieves-Aldrey & Medianero 2010; Nieves-Aldrey & Medianero in press), this paper contains the first accurate report of the genus *Disholcaspis* in the Neotropical region and includes the description of two new species from Panama.

Material and methods

Study material. The adults studied were reared from galls collected on *Quercus bumelioides* Liebm. and *Q. lancifolia* Schledl & Cham. Samplings were made and material was collected from December 2007 to May 2009 at Volcan Baru and Renacimiento, Chiriqui Province, Panama. The adult insects emerged from the galls in rearing cages under laboratory conditions.

Specimen preparation. For observation under a scanning electron microscope (SEM), adult cynipids were dissected in 70% ethanol, air dried, mounted on a stub and coated with gold. Micrographs were taken with an EVO 40 Zeiss and FEI QUANTA 200 microscope (high vacuum technique) for several standardized views. Forewings were mounted in Euparal on slides and later examined under a Wild MZ8 stereo microscope. Images of adult habitus and gall dissections were taken with a NIKON Coolpix 4500 digital camera attached to a Wild MZ8 stereo microscope. Measurements were made with a calibrated micrometer scale attached to an ocular of the light

microscope. Terminology of morphological structures and abbreviations follow Ronquist & Nordlander (1989), Ronquist (1995), Nieves-Aldrey (2001) and Liljeblad *et al.* (2008).

Description of species

Disholcaspis bettyannae **Medianero & Nieves-Aldrey sp. nov.**

(Figs. 1, 2, 5A-B & 6A-C)

Type material. Holotype ♀ (Fig. 5A) (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. Cat. nº 2108). PANAMA, Chiriquí, Volcan Baru 8º 47' 50 08" N, 82º 29' 35 9" W, 1800 m; ex gall on stems of *Quercus bumelioides* Liebm. (Fagaceae), gall collected 30.i.2008, insect emerged ii.08, E. Medianero leg. Paratypes: 3♀ same data as holotype, but collected 22.xii.2008, insect emerged i.09. Two paratypes in MNCN, one paratype in Maestría en Entomología, Universidad de Panamá (MEUP).

Additionally, 1♀ paratype of the type series was dissected for SEM observation (in MNCN).

Etymology. Named after Dra. Betty Ann Rowe Catsambanis Vice-Rector Research/Graduate Programs, University of Panama.

Diagnosis and comments. The species is closely allied to *D. quercusvirens* Ashmead from Florida, being similar in color and a majority of morphological characteristics. The species differ in notauli length, the scutellar foveae, leg coloration and, mainly, in the gall that is induced. *Disholcaspis bettyannae* has the notauli distinct posteriorly and medially, obliterated anteriorly, smooth, broad and convergent posteriorly, whereas *D. quercusvirens* has notauli weakly impressed posteriorly. The new species has scutellar foveae ellipsoidal, shallow but distinct, whereas the scutellar foveae are indistinct in *D. quercusvirens*. *Disholcaspis bettyannae* has legs yellowish brown, whereas *D. quercusvirens* has legs light reddish-brown. The new species induces a small globular gall (6- 11 mm diameter) that does not secrete nectar. Internally, it is of a compact, rather hard, corky texture and contains a free, oval yellowish larval cell (Fig. 6C), whereas *D. quercusvirens* induces similar small, globular galls, internally spongy, which exude a sticky substance that attracts ants. In coloration, *Disholcaspis bettyannae* also resembles *D. unicolor* Kinsey from Mexico

and *D. mamillana* Weld from California (USA) but differs from them mainly in the type of gall that it induces. The globular bullets (21 mm in diameter) with a nipple at the apex. Additionally, the anteroadmedian signa are not visible in *D. unicolor*, whereas they are discernible in *D. bettyannae.*

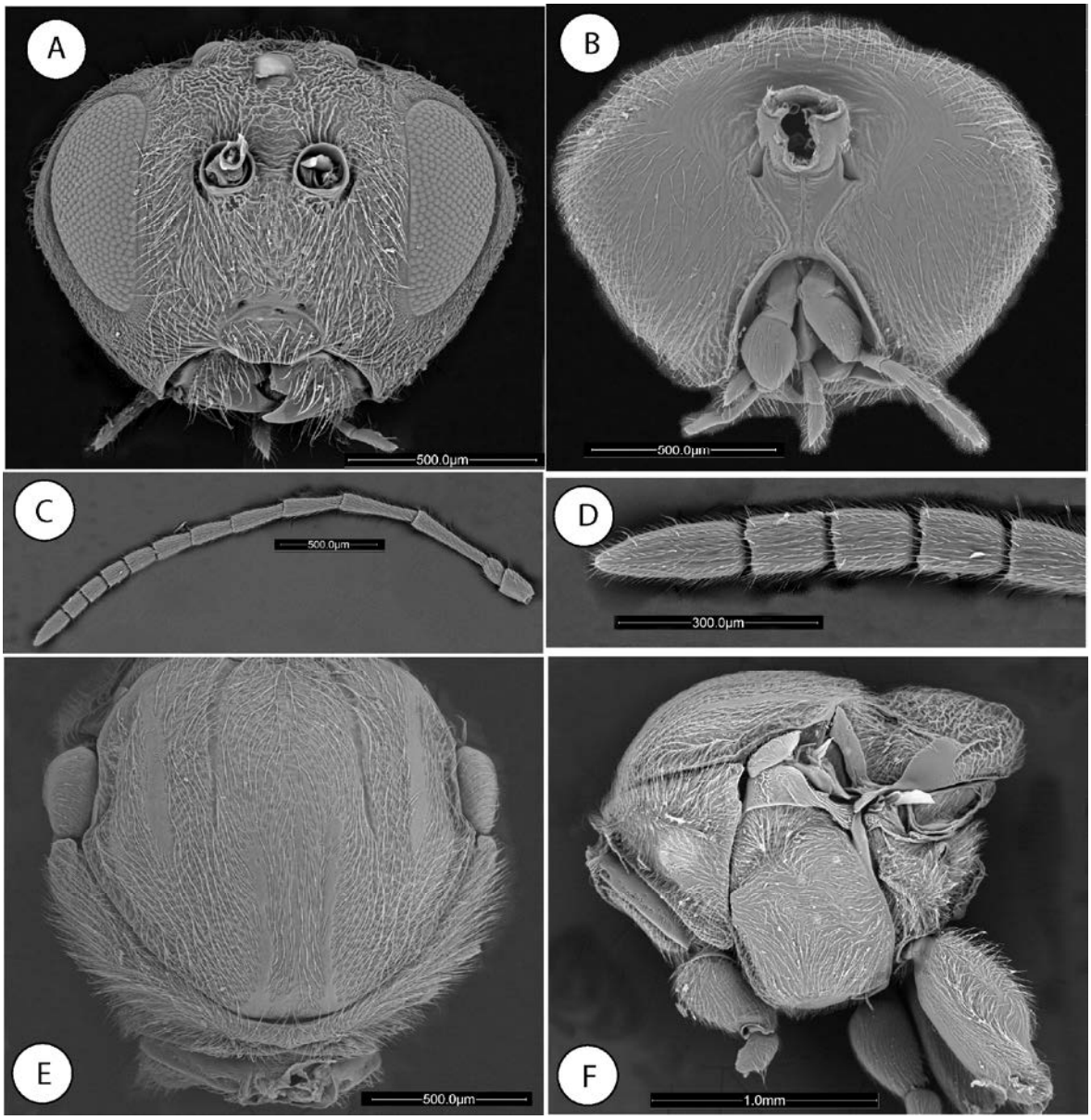

Figure 1. *Disholcaspis bettyannae*: (A) Head anterior view. (B) Head posterior view. (C) Female antenna. (D) Detail of last flagellomeres. (E) Pronotum antero-dorsal view. (D) Mesosoma lateral view.

Description. Body length 3.94 mm (range 3.64 - 4.19; N = 4) for females. Body uniformly amber and shiny with distal segment of antenna, anteroadmedian signa area, parapsidal signa, propodeal area (except by spiracular area), posteromedial area of metasoma, sternum, stipes, last segment of maxillary palp, labial palp and claws dark

brown to black. Legs yellowish brown. Forewing hyaline with some very light infumation, veins dark brown to black.

Female. Head rugose, moderately pubescent with piliferous punctures, in dorsal view about 3.4 times wider than long. POL 1.5 times longer than OOL, posterior ocellus separated from inner orbit of eye by 2.2 times its longest diameter. Head in anterior view (Fig. 1A) transversely ovate, 1.3 times wider than high, gena moderately broadened behind eyes, 0.26 times the diameter of compound eye. Vertex, frons and occiput more rugose; face, gena with piliferous punctures, irradiating carinae from clypeus delicate and short, not reaching ventral margin of compound eye and absent medially above clypeus; head moderately pubescent, with relatively long golden setae, except on vertex and frons with sparse and shorter setae. Clypeus more or less trapezoidal, 1.8 times wider than high, mostly smooth and moderately pubescent, ventral margin sinuate, slightly projecting over mandibles. Anterior tentorial pits well visible; epistomal sulcus not indicated, clypeo-pleurostomal lines visible. Malar space 0.4 times height of compound eye, without malar sulcus. Toruli situated slightly above mid-height of compound eye; distance between antennal rim and compound eye 1.1 times width of antennal socket including rim. Ocellar plate not raised. Head, posterior view (Fig. 1B) without occipital carina. Gula short; distance between occipital and oral foramina 1.5 times height of occipital foramen (Fig. 1B). Hypostomal sulci well separate at oral fossa.

Mouthparts (Figs. 1A, 1B): mandibles strong, exposed; with dense setae in base, right mandible with three teeth; left with two teeth. Cardo of maxilla not visible, maxillary stipes relatively short and broad, about 2.2 times longer than wide. Maxillary palp five-segmented. Labial palp three-segmented.

Antenna (Fig. 1C) of moderate length, as long as 1/2 body length, with 13 antennomeres; flagellum not broadening towards apex; with relatively long, erect setae, and elongate placodeal sensilla not well visible (Fig. 1D). Relative lengths of antennal segments: 18:11:40:37:28:26:21:19:14:12:12:11:22. Pedicel, sub-globose, small, 0.6 as long as scape; F1-F6 long and slender, gradually decreasing in length. F1 1.08 times as long as F2. F7-F10 short and wide, F11 2.7 times longer than wide, 2.0 times as long as F10 (Fig. 1D). Placodeal sensillae on F3-F11 disposed in one row of 8-10 sensillae in half dorsal area of each flagellomere.

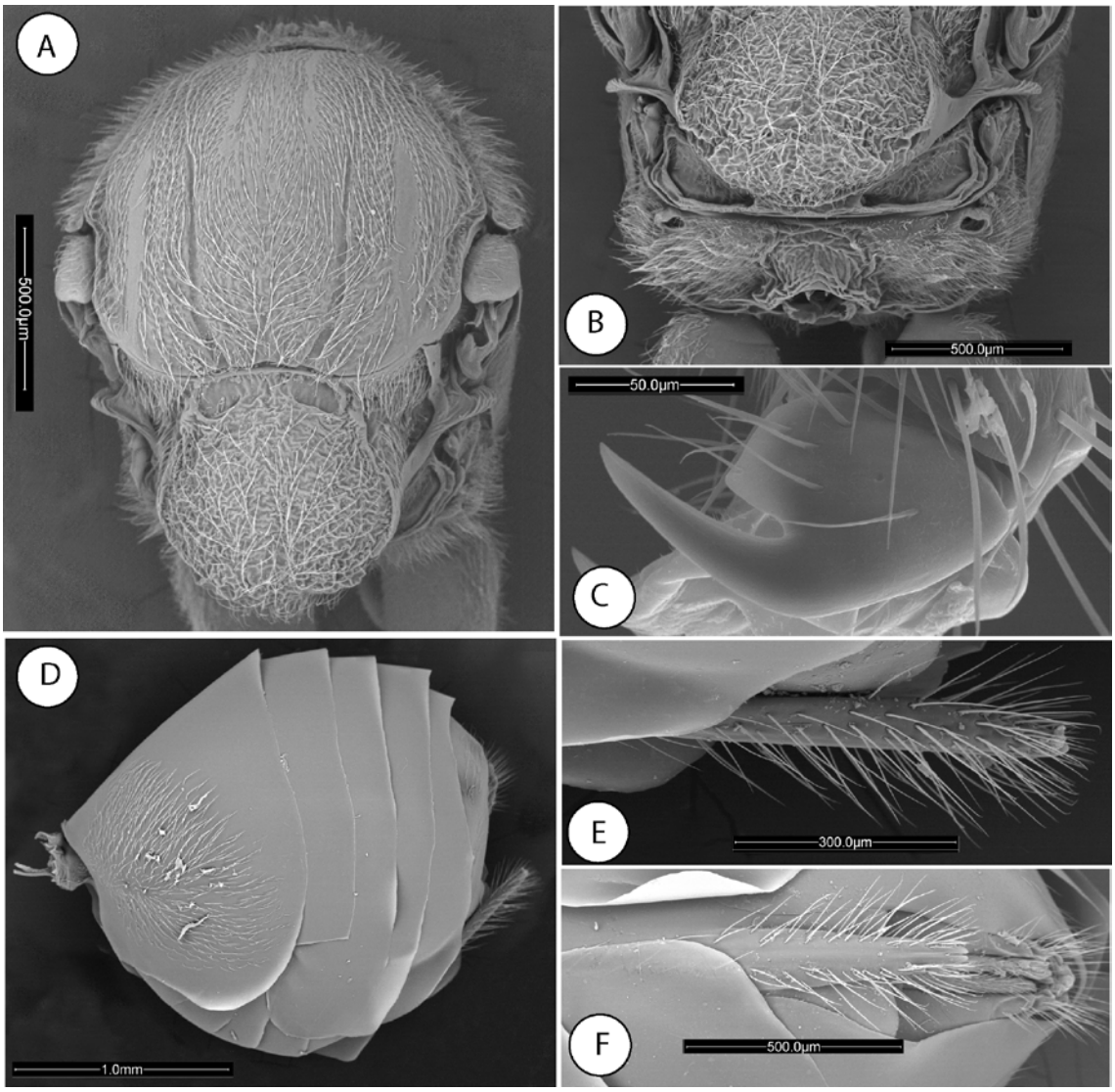

Figure 2. *Disholcaspis bettyannae*: (A) Mesosoma dorsal view. (B) Propodeum. (C) Metatarsal claw. (D) Metasoma lateral view. (E) Detail of ventral spine of hypopygium, lateral view. (F) Detail of ventral spine of hypopygium.

Mesosoma. Smooth to finely rugose, very densely pubescent with piliferous punctures, in lateral view 1.3 times as long as high, slightly convex dorsally. Pronotum, densely pubescent; lateral surface of pronotum with some longitudinal wrinkles dorsally; with long and dense setae (Fig. 1F). Pronotum short medially, ratio of length of pronotum medially/laterally = 0.18. Pronotal plate indistinct dorsally (Fig. 1E).

Mesonotum (Fig. 2A). Mesoscutum finely rugose, densely pubescent with piliferous punctures, slightly broader than long in dorsal view. Notauli are distinct posteriorly and medially, faint anteriorly, smooth and convergent posteriorly, with an indistinct median mesoscutal impression. Anteroadmedian signa clearly visible. Parapsidal signa broad, smooth. Transscutal fissure narrow, well-visible, deeply

impressed, slightly sinuate. Scutellar foveae ellipsoidal, shallow and almost smooth, indistinctly separated medially, but their anterior and posterior margins relatively well marked, about 1/8 as long as scutellum. Scutellum (Fig. 2A) rounded from above, about 0.8 as long as mesoscutum, strongly reticulate-rugose, in lateral view quite prolonged posteriorly over the dorsellum. Axillula densely pubescent, their anterior and posterior margins marked. Mesopleuron smooth, densely pubescent with piliferous punctures (Fig. 1F).

Metanotum (Fig. 2B). Metapectal-propodeal complex. Metapleural sulcus reaching posterior margin of mesopectus at about mid-height of metapectal-propodeal complex (Fig. 1F). Lateral propodeal carinae arched, poorly defined, with some secondary strong rugae laterally and dorsally on the bare median propodeal area (Fig. 2B), lateral propodeal area densely pubescent; nucha rugose.

Legs. Densely pubescent; metatarsal claws with a strong triangular basal lobe or teeth (Fig. 2C).

Forewing (Fig. 5B) as long as body, radial cell 3.2 times longer than wide; open along anterior margin; areolet small, triangular, closed and distinct. R1 and M nearly straight, not reaching wing margin. R1 and Rs weakly pigmented. Rs slightly bowed. Rs+M not reaching basalis. 2r well pigmented, slightly projected medially. Apical margin of wing with short hair fringe.

Metasoma (Fig. 2D) large, as long as head and mesosoma combined, in lateral view as wide as high. Second metasomal tergite covering about two thirds of metasoma, with a patch of dense setae in its anteromedial area. Projecting part of hypopygial spine (Fig. 2E) about 2.5 times as long as wide in ventral view (Fig. 2F); laterally with long setae, longer than spine width, but not forming an apical patch.

Gall (Fig. 6A-C). Globose or bud-shaped, with a broad base, monothalamic, densely pubescent with a velvet or felt-like surface, growing singly or in clusters of two to six galls. Pale yellowish, sometimes tinged with pink or red when fresh (Fig. 6A) and light brown when mature (Fig. 6B). Internally of a compact, rather hard, corky texture and containing a free oval yellowish larval cell, (Fig. 6C). Diameter of gall 6 to 11 mm, formed in stems of *Quercus bumelioides* Liebm. and closely resemble that of *D. simulata* Kinsey, 1922, *D. canescens* Bassett, 1890 and *D. quercussuccinipes* Ashmead, 1881 known from USA.

Distribution. *Disholcaspis bettyannae* was found between 1431-2400 m a.s.l. at

Chiriqui, Panama.

Biology. Only the asexual generation is known, inducing galls on *Quercus bumelioides* Liebm. (section Quercus). The galls are found between October and May during the dry season in Panama. The insects studied emerged in December and February.

***Disholcaspis bisethiae* Medianero & Nieves-Aldrey sp. nov.**

(Figs. 3, 4, 5C-D & 6D-F)

Type material. Holotype ♀ (Fig. 5C) (in Museo Nacional de Ciencias Naturales, Madrid, Spain, card mounted. Cat nº 2109). PANAMA, Chiriquí, Renacimiento, 8º 49' 58 7" N, 82º 44' 44 5" W, 1270 m; ex gall on stems of *Quercus lancifolia* Schledl & Cham. (Fagaceae), gall collected 22.i.2009, insect emerged 23.i.09, E. Medianero leg. Paratypes: 4♀, same data as holotype; 1♀ same data as holotype, but collected 18.vi.2008, insect emerged vii.08, E. Medianero leg. Four paratypes in MNCN, one paratype in Maestría en Entomología, Universidad de Panamá (MEUP).

Additionally, 2♀ paratype of the type series were dissected for SEM observation (in MNCN).

Etymology. Named after Biseth Araúz, wife of the first author.

Diagnosis and comments. Closely similar to *D. bettyannae* described above in color and a majority of morphological characteristics. The two species can be readily distinguished using the following key for the identification of *Disholcaspis* of Panama:

1. Female antenna with 11 flagellomeres. Frons with strong rugae; facial striae radiating from clypeus visible. Ocellar plate not raised. Scutellar foveae smooth, confluent, with anterior and posterior margins visible. 2r vein of forewing with a stump medially prolonged into the radial cell. Projecting part of hypopigial spine less than 2.5 times as long as wide. Galls on stems of *Q. bumelioides* .....***D. bettyannae***

● Female antenna with 12 flagellomeres. Frons with alutaceous sculpture and only some weak rugae; radiating striae from clypeus almost indistinct or very weak. Ocellar plate slightly raised. Scutellar foveae ellipsoidal, confluent, with some longitudinal rugae and posterior margins indistinct. 2r without a stump medially. Projecting part of hypopigial spine about three times as long as wide. Galls on stems of *Q. lancifolia*. .....***D. bisethiae***

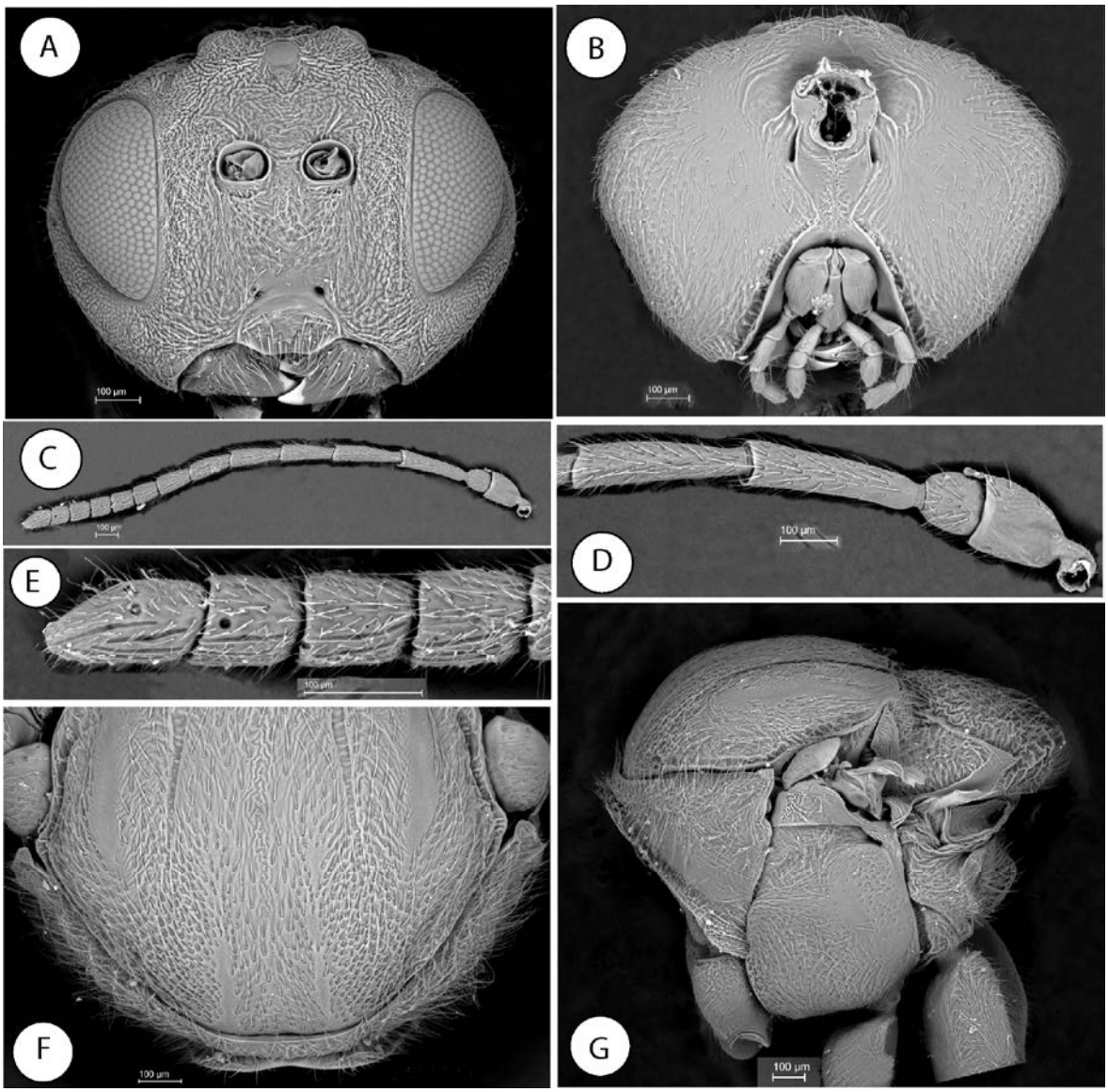

Figure 3. *Disholcaspis bisethiae*: (A) Head anterior view. (B) Head posterior view. (C) Female antenna. (D) Detail of basal flagellomeres. (E) Detail of last flagellomeres. (F) Pronotum antero-dorsal view. (G) Mesosoma lateral view.

Like *D. bettyannae, D. bisethiae* resembles in coloration *D. quercusvirens* Ashmead, *D. unicolor* Kinsey and *D. mamillana* Weld, but differs from them in the characteristics described in the diagnosis of the first described species.

Description. Female body length 3.58 mm (range 3.17-3.72; N = 6). Head, mesosoma, and metasoma shining amber to brown, with the two last segments of antenna, anteroadmedian signa area, parapsidal signa, median propodeal area, posteromedial metasoma area, sternum, last segment of maxillary palp, labial palp and claws dark brown to black. Legs yellowish brown. Forewing slightly yellowish brown, veins dark brown.

Female. Head, rudely alutaceous, strongly pubescent, with piliferous punctures, in dorsal view about 3.0 times wider than long. POL 1.75 times longer than OOL, posterior ocellus separated from inner orbit of eye by 1.6 times its longest diameter. Head in anterior view 1.27 times wider than high (Fig. 3A). Genae slightly expanded behind eyes. Vertex, frons and genae pubescent with sparse and shorter setae, face and occiput more heavenly pubescent, with relatively long setae. Clypeus trapezoidal, 1.6 times wider than high, shining alutaceous, with long setae ventrally, ventral margin slightly sinuate and projected over mandibles. Anterior tentorial pits conspicuous; epistomal sulcus indistinct, clypeo-pleurostomal lines distinct. Malar space 0.38 times height of compound eye, without malar sulcus and radiating striae from clypeus virtually absent. Distance between antennal rim of torulus and compound eye 1.07 times its width including rim. Ocellar plate slightly raised. Head, posterior view (Fig. 3B). Distance between occipital and oral foramina 1.27 times height of occipital foramen. Occiput without occipital carina, with some transversal rugae dorso-lateral to occipital foramen. Hypostomal sulci separated at hypostoma.

Mouthparts (Fig. 3B) as the preceding species, but cardo of maxillae visible.

Antenna 0.6 times as long as body (Fig. 3C); with 12 flagellomeres, flagellum not broadening towards apex; with relatively long, erect setae and elongate placodeal sensilla visible only on F4–F12. F1-F6 long and slender, gradually decreasing in length. F7-F12 short and wide. Relative lengths of antennal segments: 19:13:39:39:30:29:24:20:15:18:12:12:10:17. Pedicel, globose, small, 0.7 as long as scape; F1 as long as F2 (Fig. 3D). F12 1.9 times longer than wide, 1.7 times as long as F11 (Fig. 3E).

Mesosoma. Smooth to finely alutaceous, densely pubescent with piliferous punctures, 1.23 times broader than long in dorsal view, 1.2 times as long as high in lateral view. Pronotum as *D. bettyannae.*

Mesonotum. Mesoscutum (Fig. 4A), smooth to alutaceous, densely and uniformly pubescent, with piliferous punctures. Notauli distinct posteriorly and medially, faint anteriorly, crossed by transversal rugae, convergent posteriorly. Anteroadmedian signa and parapsidal signa visible. Median mesoscutal impression absent. Scutellum (Fig. 4A), rounded, about 0.4 as long as mesoscutum, strongly reticulate-rugose and moderately pubescent. Scutellar foveae ellipsoidal, confluent medially, with some longitudinal rugae, indistinctly margined posteriorly. Scutellum, in lateral view

extended posteriorly over the dorsellum. Mesopleuron (Fig. 3G) as the preceding species.

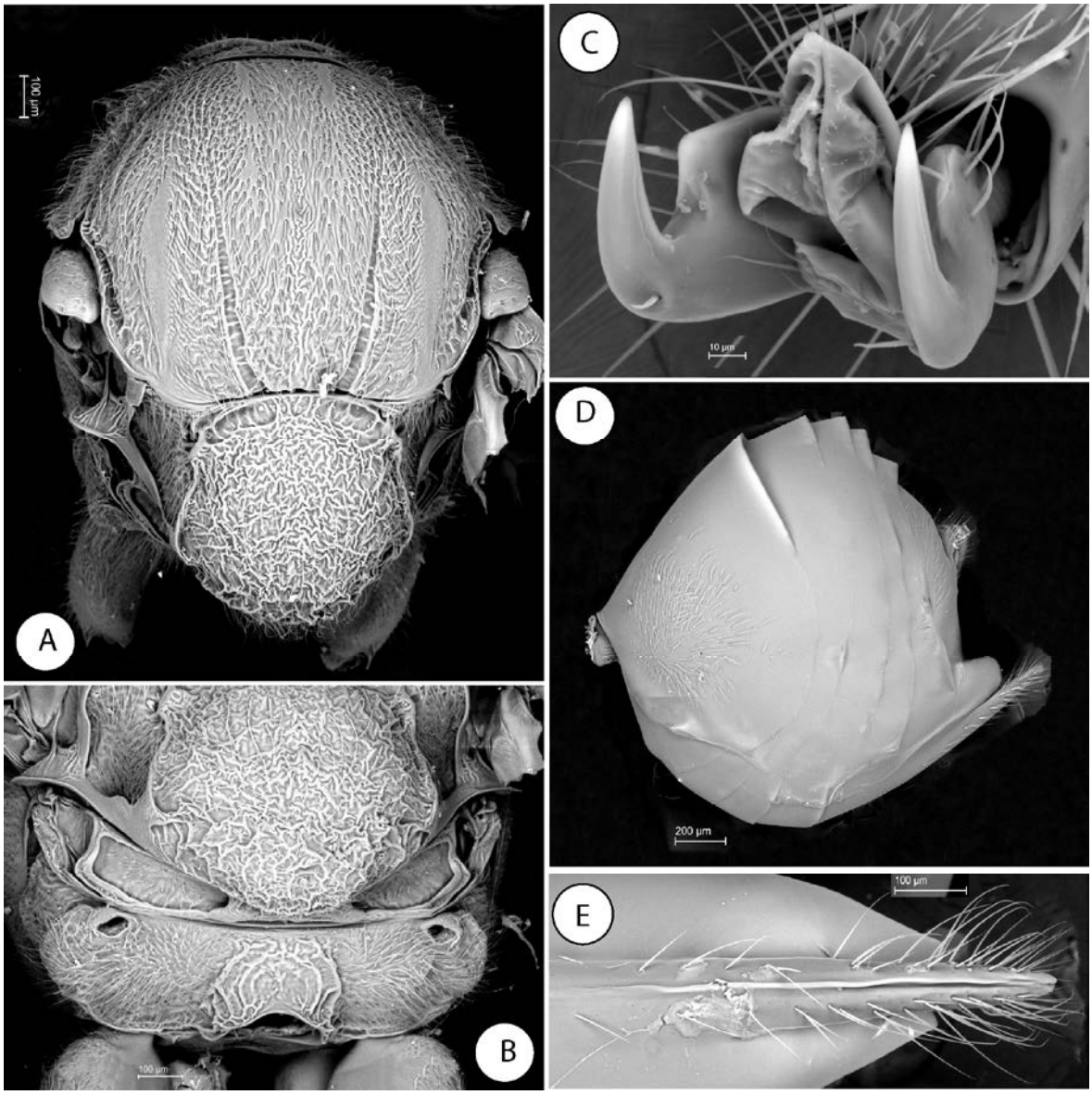

Figure 4. *Disholcaspis bisethiae*: (A) Mesosoma dorsal view. (B) Propodeum. (C) Metatarsal claw. (D) Metasoma lateral view. (E) Detail of ventral spine of hypopygium.

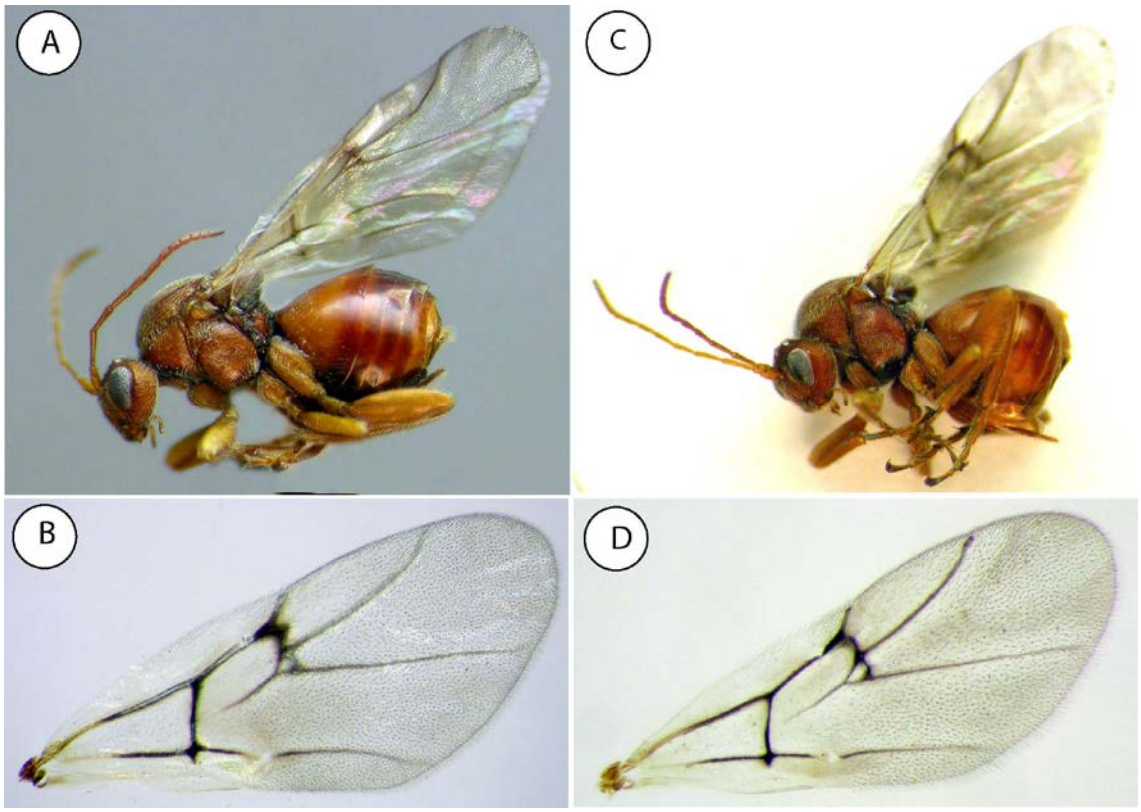

Figure 5. Habitus and forewings of *Disholcaspis* species: (A) *Disholcaspis bettyannae*, female (B) forewing of female. (C) *Disholcaspis bisethiae,* female. (D) forewing of female.

Metanotum (Fig. 4B). Metapectal-propodeal complex as *D. bettyannae*. Lateral propodeal carinae arched (Fig. 4B). Median propodeal area rugose and glabrous with arched rugae (Fig. 4B).

Legs. with metatarsal claw bearing a strong basal tooth (Fig. 4C).

Forewing (Fig. 5D). As long as body, radial cell 3.6 times longer than wide; open along anterior margin; areolet small, triangular. Rs well pigmented, slightly bowed, vein 2r slightly angulated but not prolonged by a stump into the radial cell. Hair fringe on apical margin moderately long.

Metasoma (Fig. 4D). Smooth and shiny; large, as long as head and mesosoma combined; in lateral view 1.1 times as high as long. T3 covering about 2/3 of metasoma; without micropunctures; with a patch of dense setae in its anteromedial area. Projecting part of hypopygial spine, (Fig. 4E); about 2.75 times as long as wide; lateral margins of hypopygial spine with long setae projecting over apical end of the spine, but not forming a terminal tuft.

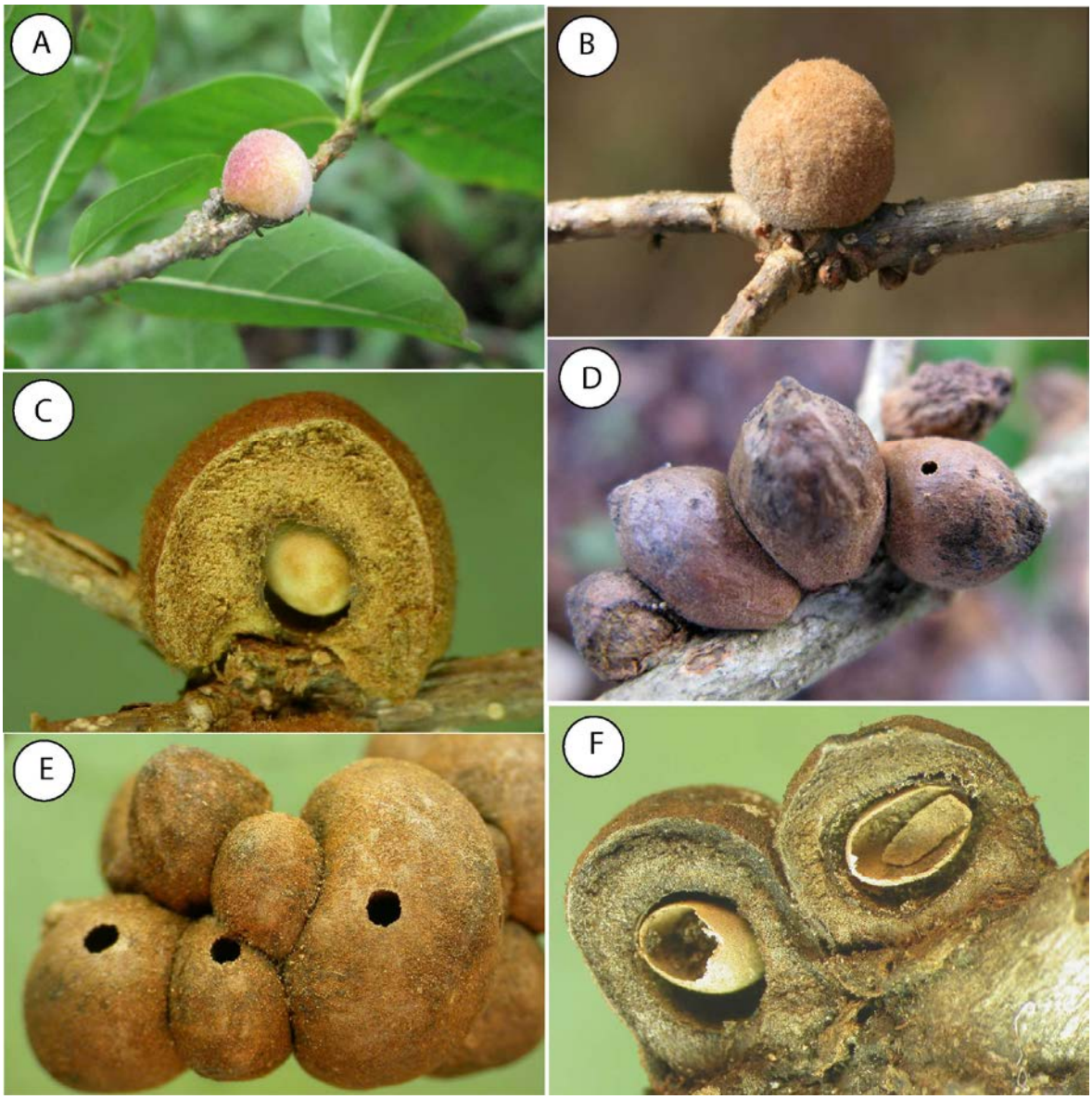

Figure 6. Galls of *Disholcaspis* species from Panama: (A) Immature gall of *Disholcaspis bettyannae*. (B) mature galls of *Disholcaspis bettyannae*. (C) Section of a gall showing the central cell. (D) Old gall of *Disholcaspis bisethiae* showing the exit holes of inducer. (E) Mature gall of *Disholcaspis bisethiae*. (F) Section of a gall showing the central cell.

Gall (Fig. 6 D-F) Globular, monothalamic, with a more or less distinct nipple at the apex of some galls; hard, with a felt-like covering, growing in clusters of two to ten galls (Fig. 6E). Brown when fresh and dark brown to black when old (Fig. 6D). Internally similar to the gall of *D. bettyannae* (Fig. 6F). Diameter 8 to 14 mm. Formed in twigs of *Quercus lancifolia* Schledl & Cham. The gall most closely resembles that of *D. mamma* Walsh, known from USA.

Distribution. *D. bisethiae* was found to 1270 m a.s.l. at Cotito, Finca Hill and Piedra de Candela, Renacimiento district, in western Panama, Chiriquí Province, near the border with Costa Rica.

Biology. Only the asexual generation of *D. bisethiae* is known, inducing detachable galls on stems of *Q. lancifolia* Schledl & Cham. Galls are found between December-April, during the dry season, and the insects emerge in the same season.

Final comments

Although the genus *Disholcaspis* had been cited for the Neotropical region (Pujade-Villar & Hanson 2006), no species had been formally described. Therefore, the two new species described herein are the first species of this genus reported for the Neotropics and represent a substantial advancement in the knowledge of their distribution and biology.

The complexity, diversity and nomenclatural instability of *Disholcaspis*, as have been demonstrated in recent studies (Melika & Abrahamson 2002; Liljeblad *et al*. 2008), together with the new information provided here, demonstrate the necessity of revising this genus. Furthermore, galls induced by the species of *Disholcaspis* are among the most complex productions of the Cynipidae (Kinsey 1920), and the inclusion of this genus in ongoing phylogenetical analysis is important in understanding the evolutionary history of oak gall wasps (Liljeblad *et al.* 2008; Stone *et al*. 2010).

Inquiline and parasitoid associated community

Unlike other galls induced by species of *Disholcaspis*, the two new species from Panama do not secrete nectar and consequently are not associated with ants. However, the galls of the two new species described host a complex of parasitoids that include representatives of the genera *Torymus* Dalman (Torymidae), *Eurytoma* Illiger, *Sycophila* Walker (Eurytomidae), *Ormyrus* Westwood (Ormyridae), *Eupelmus* Dalman

(Eupelmidae) and *Aprostocetus* Westwood (Eulophidae). Additionally, we reared two species of inquilines from the galls; *Synergus nicaraguensis* Díaz & Gallardo and a new species of this genus (Nieves-Aldrey & Medianero in press.).

Acknowledgements

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2.4-Dos nuevas especies neotropicales de avispas gallícolas de los robles del género *Loxaulus* Mayr (Hymenoptera: Cynipidae: Cynipini) de Panamá[5]

Resumen

Se describen dos nuevas especies de *Loxaulus* Mayr, *Loxaulus championi* y *Loxaulus panamensis* (Hymenoptera: Cynipidae: Cynipini) de Panamá. Las nuevas especies inducen agallas en *Quercus bumelioides* Liebm. (Fagaceae, secc. Quercus, robles blancos). Se aportan los caracteres diagnósticos, la descripción de la agalla así como la biología y la distribución de las nuevas especies. Las nuevas especies representan el primer registro del género *Loxaulus* fuera de Norteamérica.

[5] Manuscrito publicado como; Medianero, E., Nieves-Aldrey, J. L. & Melika G. 2011. Two new neotropical species of oak gall wasps of the genus *Loxaulus* Mayr (Hymenoptera: Cynipidae: Cynipini) from Panama. Zootaxa.

Two new neotropical species of oak gall wasps of the genus *Loxaulus* Mayr (Hymenoptera: Cynipidae: Cynipini) from Panama.

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Abstract

Two new species of *Loxaulus* Mayr, *Loxaulus championi and Loxaulus panamensis* (Hymenoptera: Cynipidae: Cynipini) are described from Panama. Both new species induce galls on *Quercus bumelioides* Liebm. (Fagaceae, sect. Quercus, White Oaks). The diagnostic characters, gall descriptions, distribution, and biological data on the new species are given. The new species represent the first records of the genus *Loxaulus* outside North America.

Key words: Cynipidae, oak gall wasps, *Quercus*, Chiriqui, Panama

Introduction

The nearctic genus *Loxaulus* Mayr, with 14 described species, is known only from north of Mexico, in the USA (Melika & Abrahamson 2000). Galls, similar to those of *L. boharti* Dailey & Sprenger, known from California (USA), were collected in Baja California Norte (Mexico), however, no adults were reared (Dailey & Sprenger 1983)

thus the distribution of the species in Mexico is still questionable. The representatives of the genus are distributed across USA: 5 species known only from California, 3 species – from Arizona and New Mexico, the rest of species distributed from Texas to Florida and northward along the Eastern Coast. The genus was recently reviewed by Melika & Abrahamson (2000, 2002) and according to these authors *Loxaulus* form a distinct morphological entity, that can be morphologically characterized as follows: the head is massive, broader than the mesosoma in dorsal view and usually higher than broad in anterior view; the gena broadened, visible behind the compound eye in anterior view; the malar sulcus always present, distinct; antennae with 11–12 flagellomeres; the mesosoma slightly compressed in lateral view; the mesoscutum usually finely transversely coriaceous; the mesoscutellum without foveae, with a transverse shallow depression; the central propodeal area is narrow, limited by parallel or only slightly outward bent lateral carinae and with a median longitudinal carina and/or longitudinal striae; the median longitudinal carina in some species is indistinct, fragmented but always present at least in the anterior half; the radial cell of the forewing 2.5–3.8 times as long as broad, the forewing margin with or without cilia, usually with brown, smoky spots (or stripes) along the areolet, 2r, Rs, and M; tarsal claws are simple, without a basal lobe; the ventral spine of the hypopygium is short, slender or needle-like; subapical setae are short and sparse, not reaching beyond the apex of the spine and the prominent part is never more than 3.0–3.8 times as long as broad. The genus resembles the palaearctic *Plagiotrochus* Mayr and the nearctic *Bassettia* Ashmead. Recent analyses, however, doubts the monophyletic nature of *Loxaulus* (J. Nicholls pers. comm.) and its closer phylogenetic relation with *Plagiotrochus* and *Bassettia* what we shall discuss below.

In the framework of a field study of the oak gall wasps (Cynipidae) of Panama (see also Medianero & Nieves-Aldrey 2010, Nieves-Aldrey & Medianero 2010), this paper contains the first report of the genus *Loxaulus* in Central America and includes the descriptions of two new species from Panama.

Material and methods

Study material. The adults studied were reared from galls collected on *Quercus bumelioides* Liebm. Samplings were made at Volcan Baru, Chiriqui Province, Panama and material was collected from December 2007 to August 2010. The adult insects

emerged from the galls in rearing cages under laboratory conditions.

Specimen preparation. For observation under a scanning electron microscope (SEM), adult cynipids were observed without dissection using SEM at low vacuum, without coating. Micrographs were taken using an FEI QUANTA 200 microscope (low vacuum technique). Images of adult habitus, forewings and gall dissections were taken using a NIKON Coolpix 4500 digital camera attached to a Wild MZ8 stereo microscope. Measurements were made with a calibrated micrometer scale attached to an ocular of the light microscope. The terminology of morphological structures and abbreviations follow Ronquist & Nordlander (1989), Ronquist (1995), Nieves-Aldrey (2001) and Liljeblad *et al.* (2008).

Description of species

Loxaulus championi **Medianero & Nieves-Aldrey sp. nov.**

(Figs. 1, 2 & 5A-D)

Type material. Holotype ♀ (Fig. 5A) (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. Cat. nº 2111). PANAMA, Chiriquí, Volcan Baru 8º 48' 03.5" N, 82º 30' 42.7" W, 2681 m; ex gall on stems of *Quercus bumelioides* Liebm. (Fagaceae), gall collected 17.vii.2008, insect emerged vii.08, E. Medianero leg. Paratypes: 1♀ PANAMA, Chiriquí, Volcan Baru 8º 47' 54.55" N, 82º 30' 32.5" W, 2447 m collected 26.xi.2008, insect emerged xii.08, E. Medianero leg. Paratype in Maestría en Entomología, Universidad de Panamá (MEUP).

Etymology. Named after George Champion (1851-1926) English entomologist, collector of the first cynipid galls from Panama.

Diagnosis and comments. The species resembles *L. illinoisensis* (Weld) from the United States, being similar in color and a majority of morphological characteristics. However, in *L. illinoisensis* the head is less massive from above, nearly 3.0 times or more as broad as long; the notauli are distinctly impressed at least in 2/3 of the mesoscutum length posterioly; the radial cell of the forewing distinctly shorter, maximum 2.5 times as long as broad; the

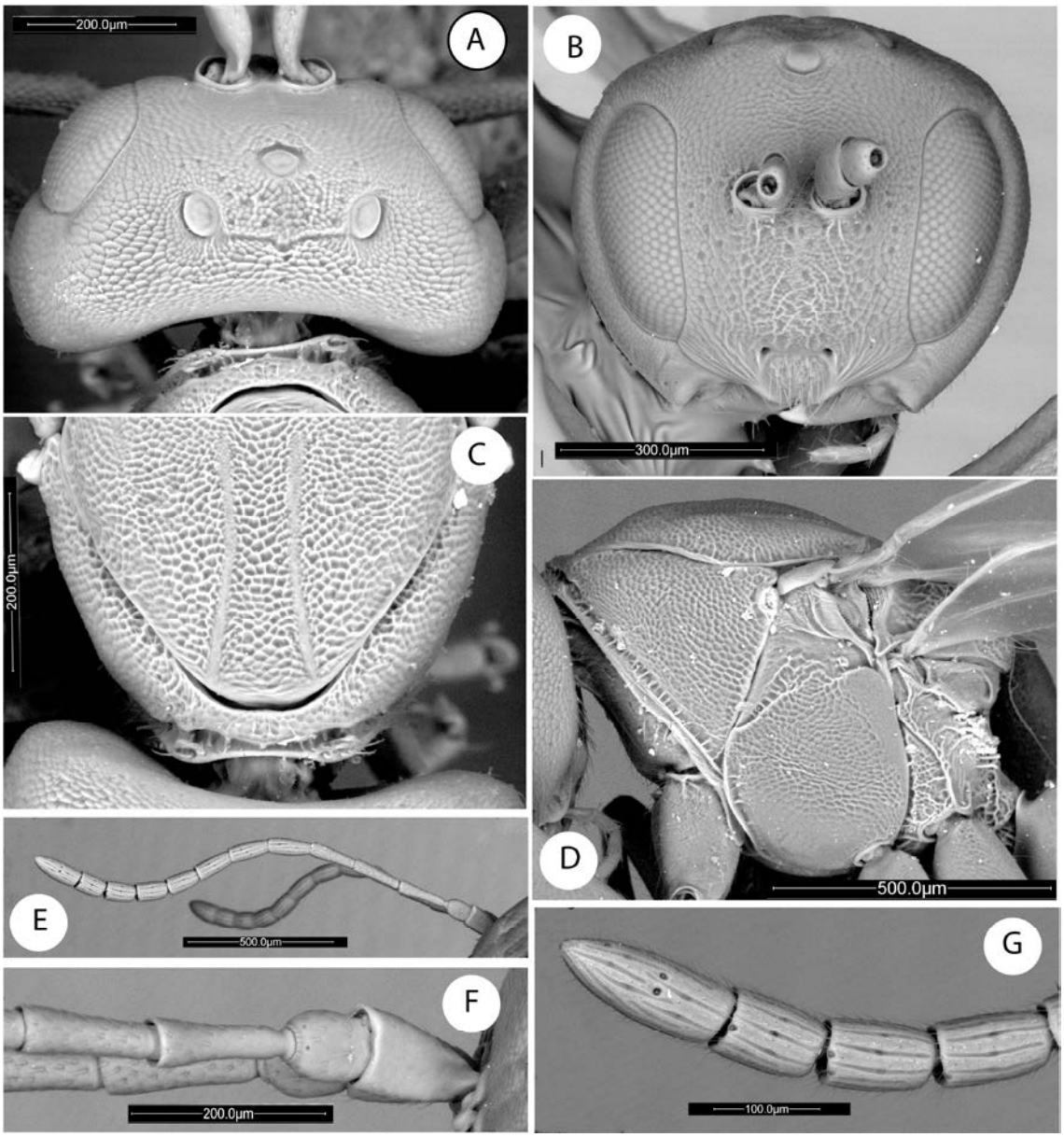

Figure 1. *Loxaulus championi*: (A) Head dorsal view. (B) Head anterior view. (C) Pronotum antero-dorsal view. (D) Metasoma lateral view. (E) Female antenna. (F) Detail of basal flagellomeres. (G) Detail of last flagellomeres.

projecting part of the hypopygial spine 2.2–2.5 times as long as wide in lateral view; currently known only from Illinois, USA, induce subterranean stem swelling-like galls, usually at the base of young sprouts of *Q. macrocarpa* Michaux. The abrupt stem swelling induced by *L. illinoisensis* is approximately 4–5 times the normal diameter of the shoot and nearly 30 cm long. Galls mature in fall and adults emerge from the end of October through November (Weld 1921).

Description. Body length 2.55 mm (range 2.5 – 2.6; N = 2) for females. Mesosoma and metasoma dark reddish-brown. Head, antennae and legs yellowish-

brown with the genae, ocelar triangle, occiput, distal half of antennae meso and metacoxae, femora and tibiae, reddish-brown. Forewing hyaline with some light infumation in and below the areolet area and on 2r vein, veins light to dark brown, with the area of 2r vein and base of radial cell darkened and lightly infuscate.

Female. Head finely coriaceous, in dorsal view about 2.0 times wider than long, 1.26 times broader than thorax. Genae strongly broadened behind eyes. POL 1.7 times longer than OOL, posterior ocellus separated from inner orbit of eye by 2.3 times its longest diameter (Fig. 1A); a longitudinal line of sculpture visible between the lateral ocelli. Head in anterior view (Fig. 1B), 1.1 times wider than high, genae strongly broadened behind eyes. Vertex, frons, lower face, gena and occiput finely coriaceous with sparse very short gold setae and weak rugae on the face, radiating striae from clypeus delicate and short, not reaching ventral margin of compound eye and absent medially above clypeus. Clypeus square with ventral margin sinuate and strongly projecting over mandibles. Anterior tentorial pits well visible; with epistomal sulcus and clypeo-pleurostomal lines slightly marked. Malar space 0.4 times height of compound eye, with a distinctive malar sulcus. Toruli situated slightly above mid-height of compound eye; distance between antennal rim and compound eye one times width of antennal socket including rim. Ocellar plate not raised. Head without occipital carina posteriorly. Occiput slightly concave. Mouthparts: mandibles not being well visible in the examined specimens, but presumably as usual in Cynipini, right mandible with three teeth; left with two teeth.

Antenna (Fig. 1E-G) of moderate length, as long as 1/2 body length, with 13 antennomeres; flagellum not broadening towards apex; with short erect setae, and placodeal sensilla visible (Fig. 1G). Relative lengths of antennal segments: 17:13:26:25:23:21:20:18:16:15:15:13:25. Pedicel, sub-globose, small, 0.7 as long as scape; F1 only slightly longer as F2 (Fig. 1F). F4-F11 longer than wide, F11 2.7 times longer than wide, 2.2 times as long as F10 (Fig. 1G). Placodeal sensillae on F4-F11 disposed in one row of 5 sensillae in half dorsal area of each flagellomere.

Mesosoma. Slightly flattened dorso-ventrally; in lateral view 1.25 times as long as high. Pronotum, scarcely pubescent; lateral surface of pronotum coriaceous without longitudinal wrinkles dorsally (Fig. 1D). Pronotum short medially, ratio of length of pronotum medially/laterally = 0.3. Pronotal plate indistinct dorsally (Fig. 1C).

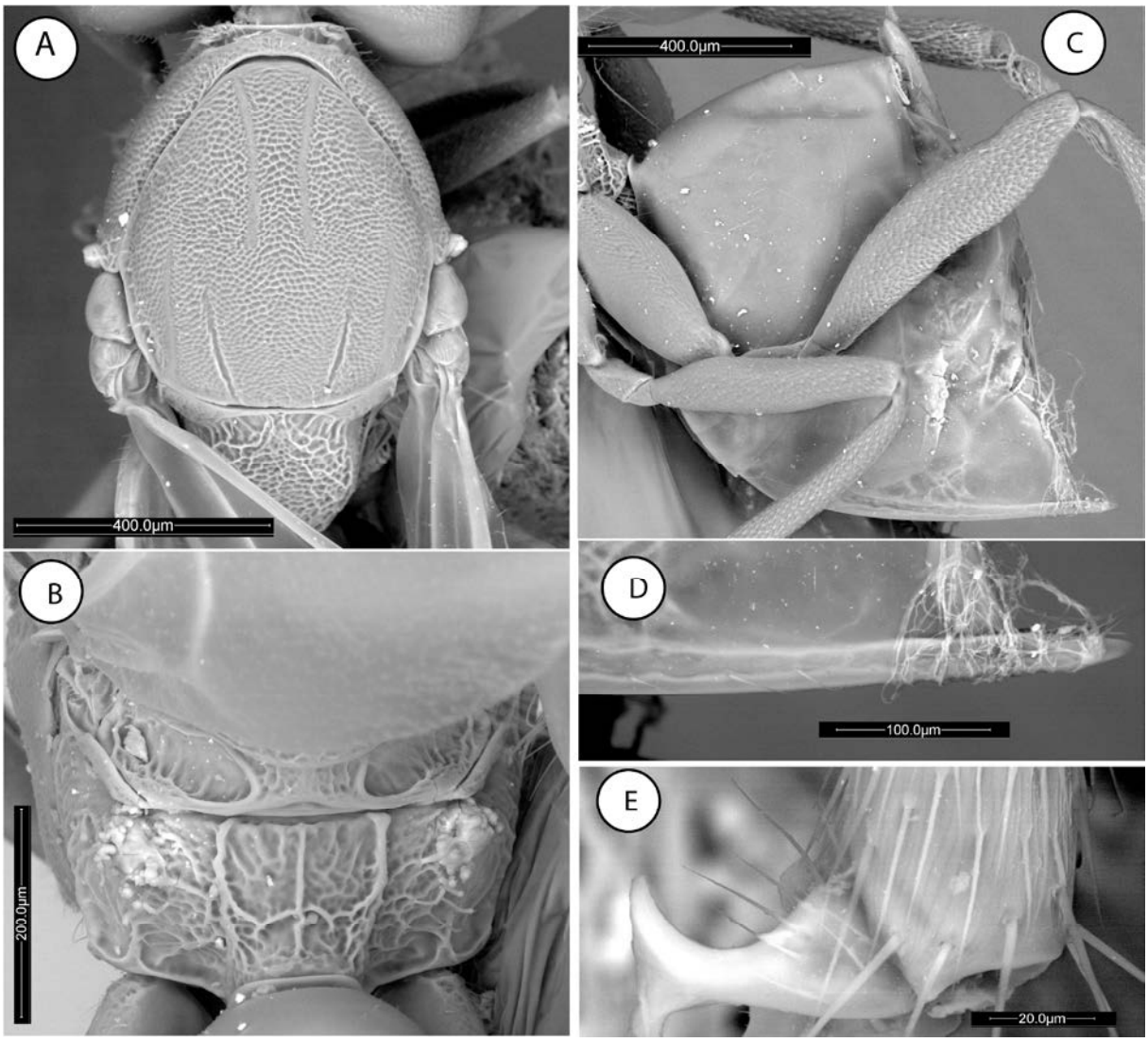

Figure 2. *Loxaulus championi*: (A) Mesosoma dorsal view. (B) Propodeum. (C) Metasoma lateral view. (D) Detail of ventral spine of hypopygium, lateral view. (E) Metatarsal claw.

Mesonotum (Fig. 2A). Mesoscutum slightly longer than broader in dorsal view, finely coriaceous and barely pubescent. Notauli distinct in posterior one third of mesoscutum, faint anteriorly and medially, widely separated at meeting of transscutal fissure, median mesoscutal impression absent. Anteroadmedian signa and parapsidal signa clearly visible. Scutellum (Fig. 2A), rounded, about 0.4 as long as mesoscutum, slightly reticulate. Scutellar foveae not well differentiated, shallow, confluent medially, with some longitudinal striae and indistinctly margined posteriorly; in lateral view the scutellum not overlapping the dorsellum. Axillula without setae, only their anterior margins marked. Mesopleuron medially with coriaceous reticulate sculpture, lacking in antero-posterior and ventral areas of mesopleuron (Fig. 1D).

Metanotum (Fig. 2B). Metapectal-propodeal complex. Metapleural sulcus reaching posterior margin of mesopectus at about two thirds height (Fig. 1D). Lateral propodeal carinae parallel, slightly branched posteriorly, a median longitudianal carinae present and complete, median propodeal area with some secondary rugae (Fig. 2B), lateral propodeal area with reticulate carinae and almost bare.

Legs. Metatarsal claws simple, with a single curved apical tooth and without basal lobes (Fig. 2E).

Forewing (Fig. 5B) slightly longer than body, radial cell 3.1 times longer than wide; open along anterior margin; areolet small, triangular, closed and distinct. Rs depigmented apically, slightly bowed and not reaching margin of wing. Rs+M not reaching basalis. Apical margin of wing with a fringe of moderately long setae. Basal cell almost bare.

Metasoma (Fig. 2C) as long as mesosoma, as high as long in lateral view. Second metasomal tergite covering about two thirds of metasoma, with line of 6-7 setae in its anteromedial area. Projecting part of hypopygial spine (Fig. 2D) about 2.8 times as long as broad in lateral view, laterally with some short setae.

Gall (Fig. 5C-D). Elongated slight swellings of twigs (Fig. 5C). The gall surface rough, of the same colour as the bark. The swellings have at least two times the diameter of a normal stem. Larval chambers are arranged longitudinally in rows under the surface of the bark (Fig. 5D). The galled stems are barely recognizable before the emergence of the adults.

Distribution. *Loxaulus championi* was found between 2400 and 2700 m a.s.l. at Volcan Baru, Chiriqui, Panama.

Biology. Only the asexual generation is known, inducing galls on *Quercus bumelioides* Liebm. (section Quercus). The galls are found between July and December during the rain season in Panama.

***Loxaulus panamensis* Medianero & Nieves-Aldrey sp. nov.**

(Figs. 3, 4 & 5E-G)

Type material. Holotype ♀ (Fig. 5E) (in Museo Nacional de Ciencias Naturales, Madrid, Spain, card mounted. Cat nº 2112). PANAMA, Chiriquí, Volcan Baru, 8°46´36.8”N, 82°31´39.3”W, 3079 m; ex gall on stems of *Quercus bumelioides* Liebm. (Fagaceae), gall collected 26.v.2010, insect emerged vi.10, E. Medianero leg. Paratypes: 1♀, same data as holotype. Paratypes: 1♀, PANAMA, Chiriquí, Volcan Baru, on *Quercus bumelioides* Liebm. (Fagaceae), collected 22.vii.2008, E. Medianero leg. One paratypes in MNCN, one paratype in Maestría en Entomología, Universidad de Panamá (MEUP).

Etymology. Named after the country where the new species was collected.

Diagnosis and comments. Closely resembles *L. championi* described above in majority of morphological characteristics. The species differs mainly by the relative length of notauli and the length of F1 and F2. *L. championi* have F2 as long as F1, whereas F2 is 1.2 times as long as F1 in *L. panamenis*. *L. championi* have notauli distinct only in posterior one third of mesoscutum whereas the notauli are complete wider and deeper in *L. panamenis*. Additionally, *L. championi* have the lateral propodeal carinae, parallel, slightly branched posteriorly, and the area between the median and the lateral propdeal carinae is rugose, whereas the lateral propodeal carinae are slightly convergent posteriorly in *L. panamenis,* and the surface between lateral and medial carinae is smooth. Another minor differences can be also noted as follows: *L. panamenis* has the lateral surface of the pronotum with some longitudinal wrinkles, radial cell 3.8 times longer than wide, with well visible infuscation below areolet, and body mostly yellowish brown, while *L. championi* has a coriaceous lateral surface of the pronotum, radial cell only 3.1 times longer than wide, with very diffuse infuscate area below areolet, and the body is mostly dark reddish–brown.

Description. Female body length 2.0 mm (N =3). Head, mesosoma, and metasoma yellowish brown with ocelar triangle, lateral surface of pronotum, scutellum (except by medial area), mesopleuron, metapectal-propodeal complex, distal half of antennae, metafemora and tibiae dark brown to black. Forewing hyaline with some very light infumation below the areolet area, veins light to dark brown, with the area of 2r vein and basalis slightly darkened.

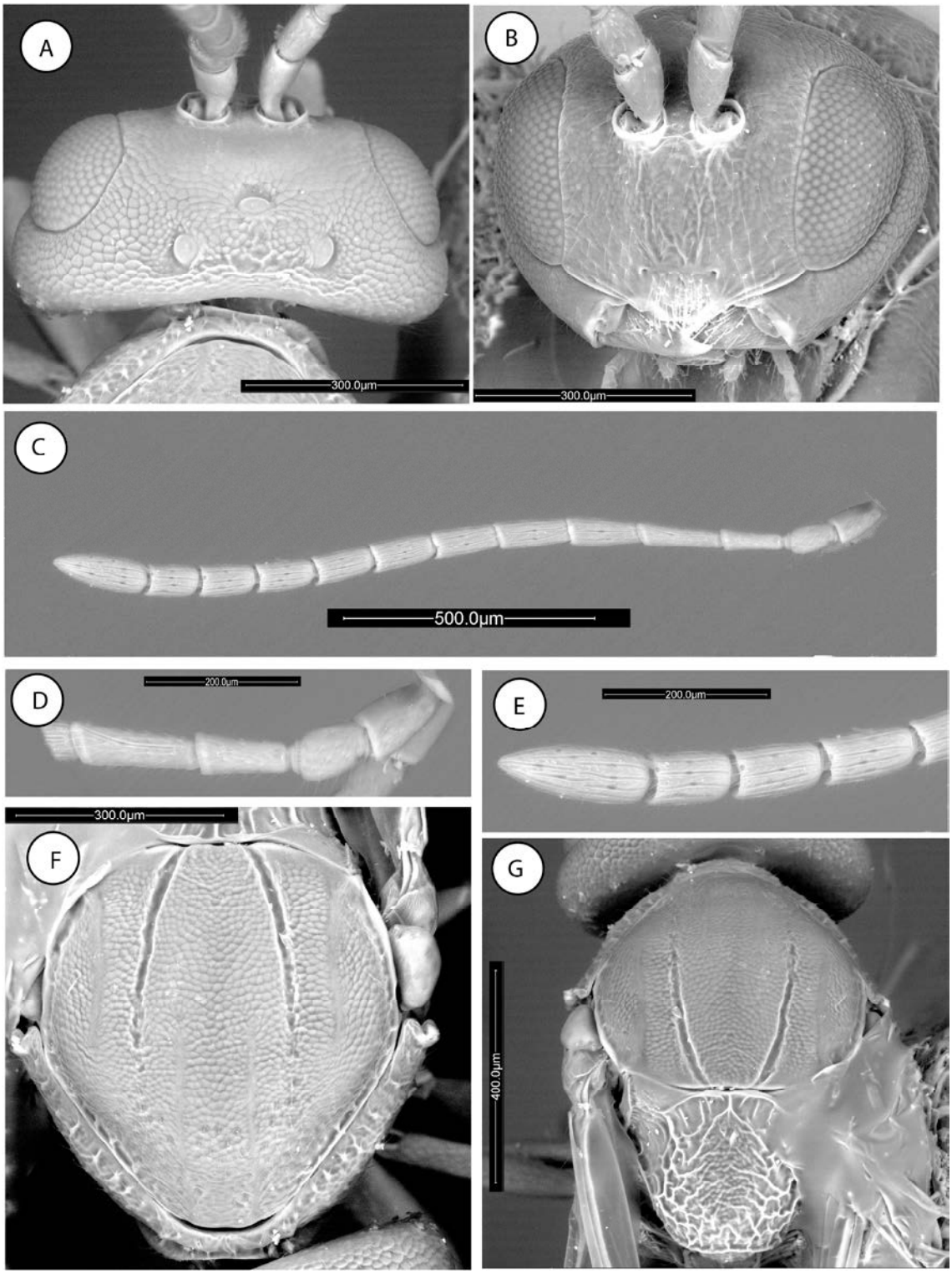

Figure 3. *Loxaulus panamensis*: (A) Head dorsal view. (B) Head anterior view. (C) Female antenna. (D) Detail of basal flagellomeres. (E) Detail of last flagellomeres. (F) Pronotum antero-dorsal view. (G) Mesosoma dorsal view.

Female. Head coriaceous, in dorsal view about 2.2 times wider than long, 1.14 times broader than thorax. Genae strongly broadened behind eyes. POL 1.3 times longer than OOL, posterior ocellus separated from inner orbit of eye by 2.6 times its longest diameter (Fig. 3A). Head in anterior view (Fig. 3B), ovate, 1.3 times wider than high. Vertex, frons, face, gena and occiput coriaceous with sparse gold setae on the face and vertex, radiating striae from clypeus absent. Clypeus square, coriaceous and moderately pubescent with ventral margin sinuate and slightly projecting over mandibles. Anterior tentorial pits well visible with epistomal sulcus and clypeo-pleurostomal lines slightly marked. Malar space 0.4 times height of compound eye, with a distinctive malar sulcus. Toruli situated slightly above mid-height of compound eye; distance between antennal rim and compound eye one times width of antennal socket including rim. Ocellar plate not raised. Head, posterior view without occipital carina. Mouthparts (Fig. 3B), mandibles strong, exposed; with dense setae in base.

Antenna (Fig. 3C-E) of moderate length, as long as 1/2 body length, with 13 antennomeres; flagellum not broadening towards apex; with short erect setae, and elongate placodeal sensilla visible (Fig. 3C). Relative lengths of antennal segments: 16:15:20:25:21:21:19:18:17:17:16:15:29. Pedicel, 0.9 as long as scape, 1.4 as long as wide;. F1 0.8 times as long as F2 (Fig. 3D). F4-F11 longer than wide, F11 2.9 times longer than wide, 2.1 times as long as F10 (Fig. 3E). Placodeal sensillae on F3-F11 disposed in one row of 5 sensillae in half dorsal area of each flagellomere.

Mesosoma. Coriaceous, in lateral view 1.25 times as long as high, slightly convex dorsally (Fig. 4A). Pronotum, scarcely pubescent; lateral surface of pronotum coriaceous with longitudinal wrinkles dorsally (Fig. 4A). Pronotum short medially, ratio of length of pronotum medially/laterally = 0.4. Pronotal plate indistinct dorsally (Fig. 3F).

Mesonotum (Fig. 3G). Mesoscutum coriaceous and barely pubescent, slightly longer than broader in dorsal view. Notauli percurrent, although slightly faint in anterior one third of mesoscutum, slightly convergent posteriorly, at meeting of transscutal fissure; median mesoscutal impression absent. Anteroadmedian signa and parapsidal signa clearly visible. Transscutal fissure narrow, well-visible, deeply impressed, slightly sinuate. Scutellum, scutellar foveae (Fig. 4B), axillula and mesopleuron (Fig. 4A) as in *L. championi*.

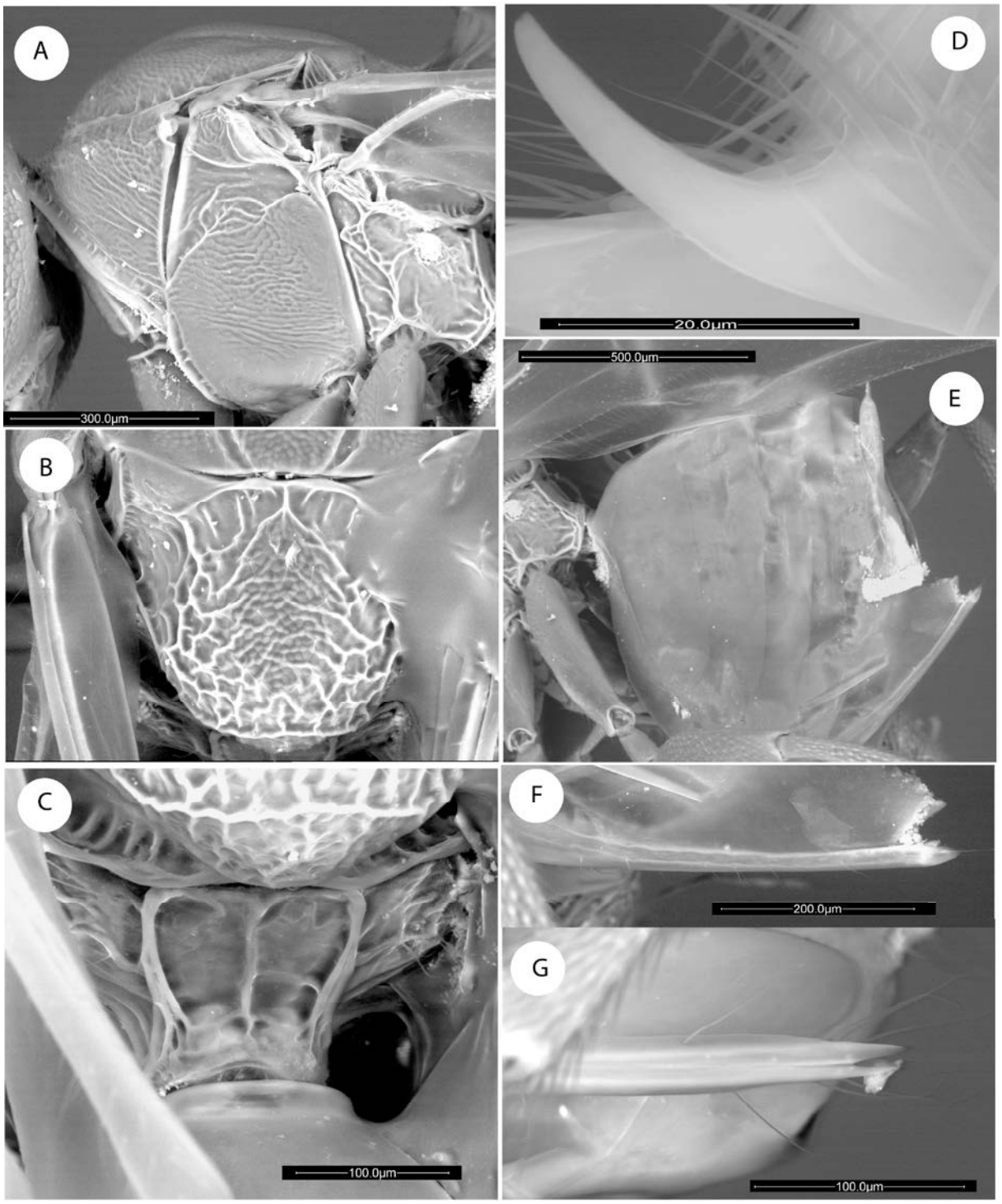

Figure 4. *Loxaulus panamensis*: (A) Mesosoma lateral view. (B) Scutellum. (C) Propodeum. (D) Metatarsal claw. (E) Metasoma lateral view. (F) Detail of ventral spine of hypopygium, lateral view. (G) Detail of ventral spine of hypopygium.

Metanotum (Fig. 4C). Metapectal-propodeal complex. Metapleural sulcus reaching posterior margin of mesopectus at about two thirds height (Fig. 4A). Lateral propodeal carinae subparallel, slightly convergent and not branched posteriorly, median longitudinal carinae present and complete, median propodeal area smooth (Fig. 4C), lateral propodeal area with reticulate carinae and almost bare.

Legs. metatarsal claws simple, without a strong triangular basal lobe or teeth (Fig. 4D).

Forewing (Fig. 5F) slightly longer than body, radial cell 3.8 times longer than wide; open along anterior margin; areolet small, triangular, closed and distinct. M nearly straight, not reaching wing margin. Rs slightly bowed. Rs+M not reaching basalis. Rs and M unpigmented. Apical margin of wing with hair fringe.

Metasoma (Fig. 4E) as in *L. championi.* Projecting part of hypopygial spine about 2.9 times as long as wide in lateral view (Fig. 4F), with some sparse long setae not reaching apex spine (Fig. 4G).

Gall (Fig. 5G). Cryptic, polythalamous in twigs. There is a only a slight stem hyperthrophy and the galls are barely detected before adults emergence. The gall consist of small ellipsoidal larval cells inside of twigs.

Distribution. *Loxaulus panamensis* was found to 3079 m a.s.l. at Volcan Baru, Chiriqui, Panama.

Biology. Only the asexual generation is known, inducing galls on *Quercus bumelioides* Liebm. (section Quercus). The galls are found between May and July during the rain season in Panama.

Key for the identification of *Loxaulus* of Panama:

1. Female antennae with first flagellomere as long as second (Fig. 1F). Notauli incomplete, distinct only in posterior one third of mesoscutum (Fig. 2A). Base of radial cell and area below areolet clearly infuscated. Median propodeal area with rugose sculpture.. Body mostly dark reddish-brown ..... ***L. championi***

● Female antenna with first flagellomere clearly shorter than second. (Fig. 3D). Notauli percurrent, clearly impressed at least in posterior two thirds of mesoscutum (Fig. 3G). Base of radial cell and area below areolet only weakly infuscated. Median propodeal area smooth (Fig. 4C). Body mostly yellowish brown ..... ***L. panamensis***

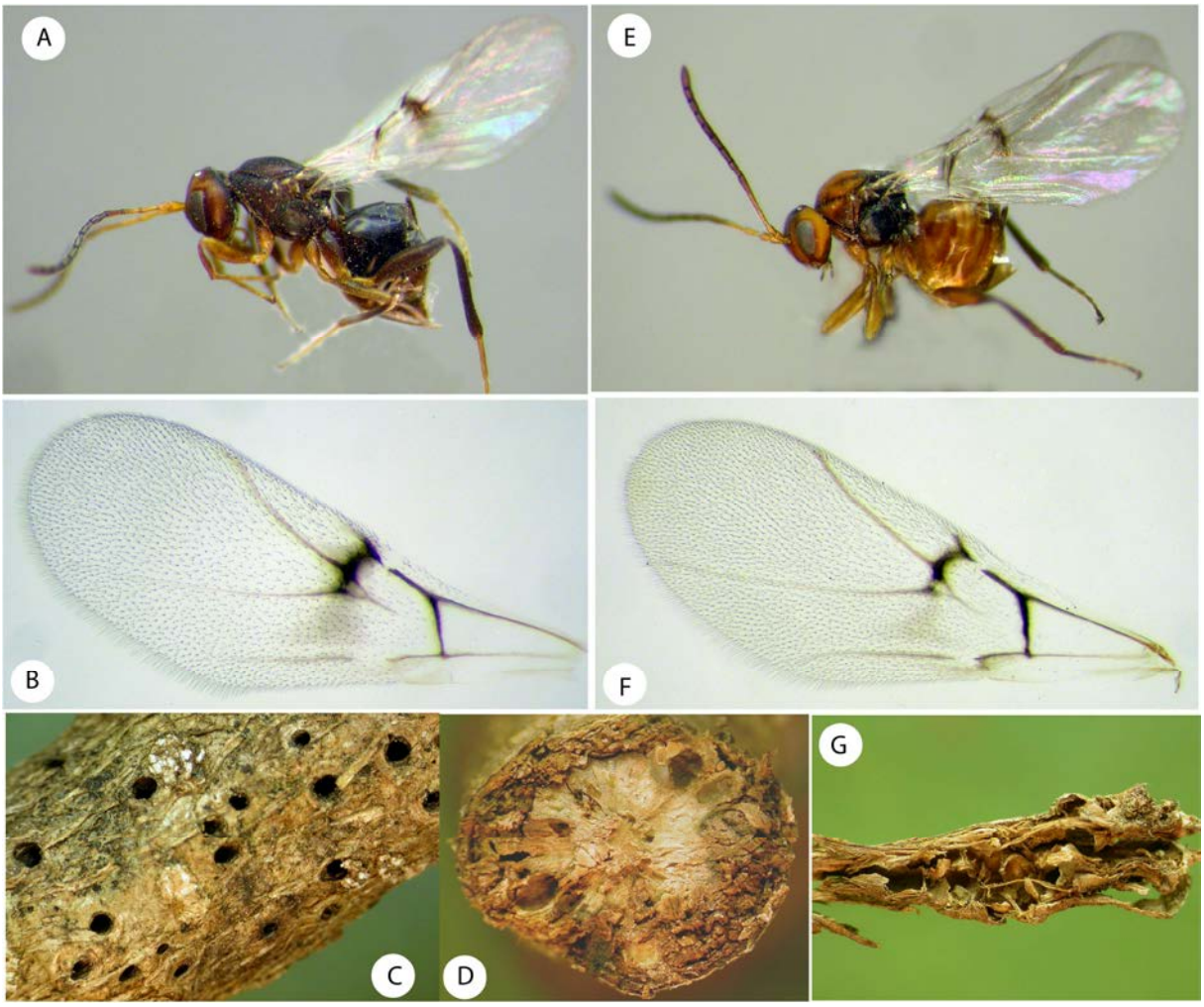

Figure 5. Habitus. forewings and galls of *Loxaulus* species: (A) *Loxaulus championi*, female (B) forewing of female. (C) mature galls of *Loxaulus championi*. (D) Section of a gall showing the cells. (E) *Loxaulus panamensis,* female. (F) forewing of female. (G) mature galls of *Loxaulus panamensis* showing the cells.

Final comments

Based on the adult, gall morphology and host associations with section Quercus (white oaks) of *Quercus*, the two herein described species of *Loxaulus* from Panama, *L. championi* and *L. panamensis*, belong to the "core" species group of the genus. Adults morphology, the type and the location of galls, with host associations of currently known 16 *Loxaulus* species suggest us that it might be a polyphyletic group. 12 species out of 16, induce galls on white oaks, while one species, *L. beutenmuelleri* Weld, known to induce leaf galls on red oaks, *Q. rubra* L. and other 3 species, *L. boharti* Dailey & Sprenger, *L. brunneus* (Ashmead), and *L. trizonalis* Weld [all known exclusively from California (USA)] associate with golden cup oaks only. Recent phylogenetic analyses had showed a deep evolutionary split between gallers on different oak sections (Stone *et al*. 2009; Melika *et al*. 2010). Thus, the genus *Loxaulus* and its limits must be carefully revised.

The genus *Loxaulus* closely resembles in its morphology the plesiomorphic traits of Palaearctic *Plagiotrochus* and the entire Nearctic *Bassettia* genus, especially what concern the massive head, dorsolaterally compressed mesosoma, usually transversely rugose mesoscutum, the structure of the central propodeal area and the structure and location of the galls they induce. All the species of *Plagiotrochus* are known to associate with the Cerris section of *Quercus* (*Q. cerris* L., *Q. brantii* Lindl., *Q. semicarpifoliae* Sm.) and the Ilex subgroup of evergreen oaks within the Cerris section in the Mediterranean region of Europe. The morphological peculiarities in the plesiomorphic species of *Plagiotrochus* from one hand and *Loxaulus* and *Bassettia* from other, seems to be convergencies and adaptations to the life history: the above-mentioned morphological features of adult's morphology are adaptations which help the adult wasps easier to move and chew out their way from the twigs (stems) where they develop. The genus *Bassettia*, all species of which known to induce stem swelling-like galls in twigs of white oaks only, might be a sister group to *Loxaulus*, at least to those species which known to induce stem galls in white oaks across the USA. Whether *Loxaulus* is a mono- or polyphyletic group [which is more probable], a further detail revision will solve.

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2.5-El género *Odontocynips* Kieffer (Hymenoptera: Cynipidae: Cynipini) en Panamá, con redescripción de *Cynips championi* Cameron 1883[6]

Resumen

Se cita por primera vez para Panamá el género *Odontocynips* Kieffer, 1910 (Hymenoptera: Cynipidae: Cynipini), incluyendo dos especies: *Odontocynips championi* (Cameron) y *O. hansoni* Pujade-Villar, que inducen agallas en *Quercus bumelioides* Liebm. y *Q. lancifolia* Schledl & Cham. (Fagaceae, sect. Quercus, robles blancos), respectivamente. *Odontocynips championi* se describió, solo a partir de sus agallas, como *Cynips championi* Cameron. En este trabajo se redescribe la especie, se describen por primera vez los adultos, se designa un Neotipo y se establece una nueva combinación taxonómica al transferirla al género *Odontocynips*. Por otra parte, se amplía la distribución geográfica y rango de hospedador de *O. hansoni*, previamente citada sólo de Costa Rica.

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The genus *Odontocynips* Kieffer (Hymenoptera: Cynipidae: Cynipini) in Panama, with redescription of *Cynips championi* Cameron 1883

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Abstract

The genus *Odontocynips* Kieffer 1910 (Hymenoptera: Cynipidae: Cynipini) is recorded for the first time in Panama, including two species, *O. championi* (Cameron) and *O. hansoni* Pujade-Villar, that induce galls on *Quercus bumelioides* Liebm. and *Q. lancifolia* Schledl & Cham. (Fagaceae, sect. Quercus, White Oaks), respectively. *Odontocynips championi* was previously described as *Cynips championi* Cameron based solely on galls. In this study, the species is redescribed, including the description for the first time of the adults, a neotype is designated and a new combination is established.. The known distribution and host range of *O. hansoni,* recorded only from Costa Rica, are also expanded upon.

Key words: Cynipidae, oak gall wasps, *Quercus*, Chiriqui, Panama, *Cynips championi*.

Introduction

Morphological and molecular analyses support the monophyly of the tribe Cynipini (oak gall wasps). This tribe, together with the Diplolepidini, Eschatocerini and Pediaspidini, forms a large group of cynipid gall-inducers restricted to woody representatives of the eudicot subclass Rosidae (Kinsey, 1920; Liljeblad & Ronquist, 1998; Liljeblad *et al*., 2008). The homoplasy, or the difficulty to detect sinapomorfic characters, in Cynipini is the most important problem in defining the correct distinctions among the different genera (Liljeblad & Ronquist, 1998; Melika & Abrahansom, 2002). For instance, recent studies of neotropical Cynipini found species that share characters of the genera *Bassettia* Ashmead, 1887; *Loxaulus* Mayr, 1881; *Callirhytis* Foerster, 1869 and *Plagiotrochus* Mayr, 1881 (Medianero & Nieves-Aldrey, 2010); other species share characters of the genera *Cynips,* Linnaeus, 1758; *Dryocosmus* Giraud, 1859 and *Trigonaspis* Hartig, 1840 (Medianero & Nieves-Aldrey, unpublished data), and still, other species could not be classified within any genus of this tribe. Thus, it can be very difficult to place a neotropical specimen within a particular genus of Cynipini.

Odontocynips Kieffer, 1910, is a peculiar genus of the Cynipini tribe confined to America. It was initially only described on the basis of adults captured in Georgia, USA (Kieffer, 1910). Later, Beutenmüeller (1918) established the relationship between the adults and their galls on the roots of white oaks. The most important character defining this genus is the presence of a large blunt lobe or tooth on the distal half of its hind femur. The type species of this genus, *O. nebulosa* Kieffer, 1910, is also characterized as showing a conspicuous pubescence on the metasomal tergites, a long projection of the hypopygial spine (approximately 5- to 6-times as long as broad in lateral view) (Fig. 4G), parallel lateral propodeal carinae, wings with infumate areas, antennae with 15 segments and simple metatarsal claws (Kieffer, 1910; Weld, 1952). Phylogenetically, *Odontocynips* is deeply nested within the *Andricus* lineage (Liljeblad *et al.,* 2008). Some biological aspects of *O. nebulosa* have been published by Wilson *et al.* (2000).

Ondontocynis was a monotypic genus until 2008, when *O. hansoni* Pujade-Villar was described from Costa Rica. The inclusion of this species in *Odontocynips* is problematic because *O. hansoni* only shares with *O. nebulosa* the presence of the large blunt lobe on the distal half of its hind femur but differs in most other morphological and biological characters (Pujade-Villar, 2008).

Andricus (*Cynips*) *championi* Cameron, 1883, was the only cynipid species

described from Panama until recently. This species was described on the basis of galls collected on twigs of an unidentified oak by George Champion in Panama. The inducing gall wasp was unknown by the describer. According to Champion´s itinerary, these galls were collected in 1882 in Chiriqui (Champion, 1907; Heckadon-Moreno, 2006). Since its determination, the taxonomic status of *Andricus* (*Cynips*) *championi* has been problematic (see Ashmead, 1899; Dalla Torre & Kieffer, 1910; Crawford, 1915; Weld, 1921; Pujade-Villar, 2008) and is considered to be *incertae sedis* (Pujade-Villar *et al.,* 2009).

This paper provides an accurate description of two species collected in Panama, belonging to *Odontocynips*. In addition, a redescription of *Andricus (Cynips) championi,* including the first description of the adults, and a new combination to *Odontocynips* genus are reported, and the neotype for this species is designated.

Materials and methods

Study material. The adults studied were reared from galls collected on *Quercus bumelioides* Liebm and *Quercus lancifolia* Schledl & Cham. (Fagaceae, sect. *Quercus*). Samplings were conducted and material was collected from December 2007 to August 2010 at Volcan Baru and Boquete, Chiriqui Province, Panama. The adult insects emerged from the galls in rearing cages under laboratory conditions. Voucher adult specimens and their galls were deposited in the entomology collections of the Museo Nacional de Ciencias Naturales, Madrid (Spain) (MNCN) and Maestria en Entomologia, Universidad de Panama (MEUP).

Specimen preparation. For observation under a scanning electron microscope (SEM), adult cynipids were dissected in 70% ethanol, air-dried, mounted on a stub and coated with gold. Micrographs were taken with an EVO 40 Zeiss microscope, using a high vacuum technique, for several standardized views. Forewings were mounted in Euparal on slides and later examined under a Wild MZ8 stereomicroscope. Images of the adult habitus and gall dissections were taken with a NIKON Coolpix 4500 digital camera attached to a Wild MZ8 stereomicroscope. Measurements were made with a calibrated micrometer scale attached to an ocular of the light microscope. Terminology of morphological structures and abbreviations follow Ronquist & Nordlander (1989),

Ronquist (1995), Nieves-Aldrey (2001) and Liljeblad *et al.* (2008).

Results

***Odontocynips championi* (Cameron, 1883) Medianero & Nieves-Aldrey n. comb.** (Figs. 1, 2 & 5A-D)

Cynips championi Cameron, 1883. Biologia Centrali-America. Vol. 1: 70.

Andricus championi (Cameron): Ashmead, 1899. Entomological News, 10: 193. (non Cameron, 1883).

Cynips championi Dalla Torre & Kieffer, 1910. Cynipidae. 446.

Cynips championi Crawford, 1915. Proceedings of the United States National Museum, 48: 580.

Cynips championi Weld, 1921. Proceedings of the United States National Museum, 59: 212.

Andricus championi Pujade-Villar, 2008. Dugesiana, 15: 79.

Andricus championi Pujade-Villar, 2009. Neotropical Entomology, 38:809.

Study material. Neotype ♀ is designated here (Fig. 5A): PANAMA, Chiriquí, Volcan Baru, 8º 46' 36 08" N, 82º 31' 39 3" W, 3079 m; ex., gall on stems of *Quercus bumelioides* Liebm (Fagaceae), gall collected 22.xii.2008, insect emerged i.2009, E. Medianero leg. Deposited in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN). Other material from type series**:** 1 ♀, same data as the neotype; 2 ♀, same data but collected 27.i.2009, insect emerged ii.2009. One ♀ in Maestría en Entomología, Universidad de Panamá (MEUP); remaining females in MNCN.

Additionally, 1 ♀ from the type series was dissected for SEM observation (in MNCN).

Diagnosis and comments. This species is closely allied to *O. hansoni* Pujade-Villar from Costa Rica, being similar in color and in a majority of morphological characters. The species differ mainly in the sculpture of the scutellum, the form of the lateral propodeal carinae, the relative length and width of F12 and the shape of the metatarsal claw. *Odontocynips hansoni* has a thoroughly and strongly reticulate-rugose scutellum that is slightly emarginate at the posterior margin and large and deep scutellar foveae clearly separated by a septum with their anterior and posterior margins marked

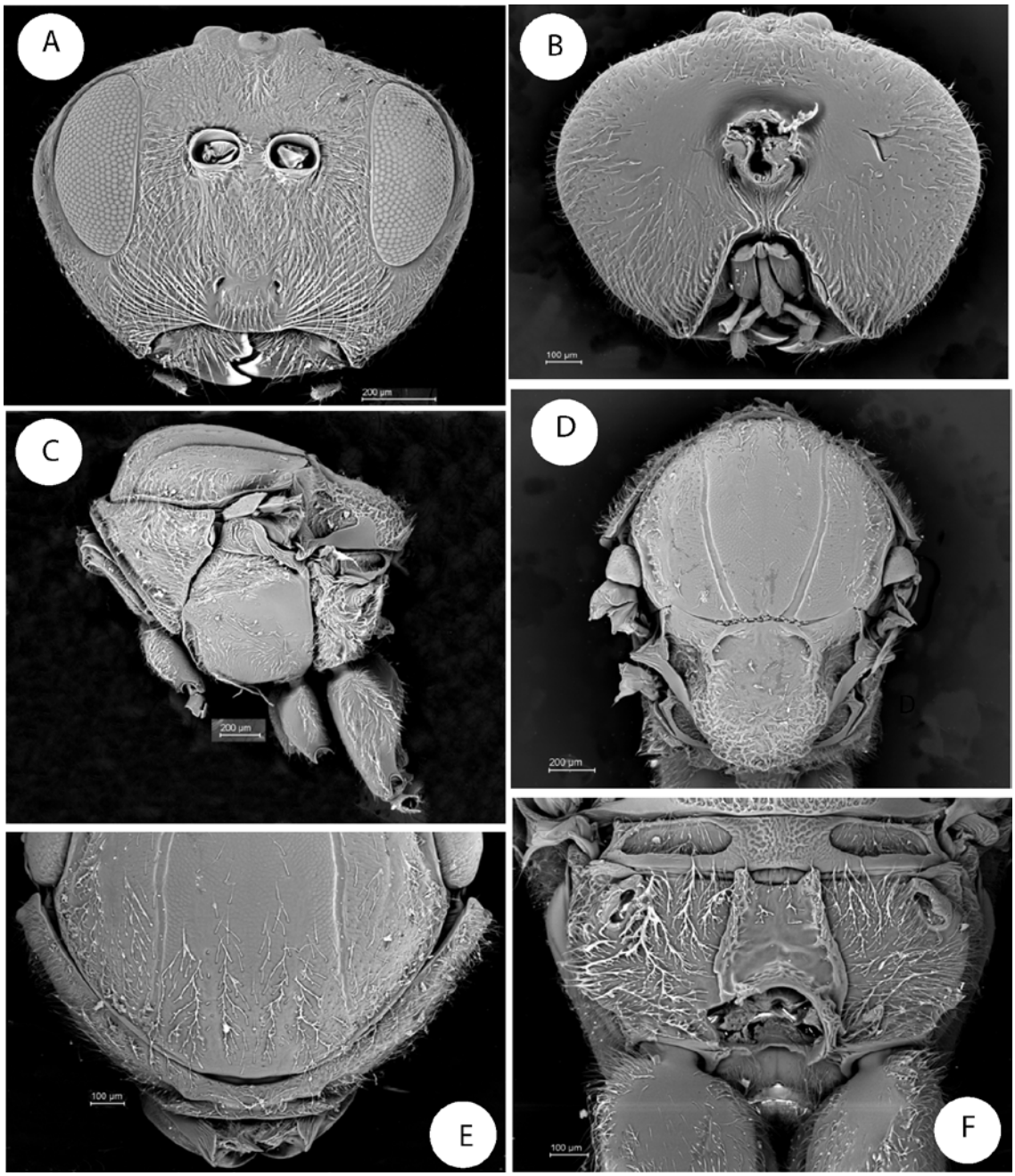

Figure 1. *Odontocynips championi*: (A) Head anterior view. (B) Head posterior view. (C) Mesosoma lateral view. (D) Mesosoma dorsal view. (E) Pronotum antero-dorsal view. (F) Propodeum.

(Fig. 3B); whereas in *O. championi,* the scutellum is slightly to moderately reticulate-rugose, anteriorly smooth, with a posterior margin that is not emarginate and scutellar foveae that are deep but not separated by a septum and with their posterior margins unmarked (Fig. 1D). Additionally, *O. championi* has simple metatarsal claws (Fig. 2E), F12 is 2.2-times longer than it is wide and 1.8-times as long as F11, an only weakly setose mesoscutum, and the median propodeal area is longer and narrow, with lateral propodeal carinae only moderately divergent. In *O. hansoni,* the metatarsal claws have one short but distinct lobe (Fig. 3F), F12 is only is 1.6-times longer than it is wide and 1.7-times as long as F11 (Fig. 3D), the mesoscutum is strongly setose, and the median propodeal area is shorter and wider, with the lateral propodeal area strongly divergent (Fig. 3E).

Redescription. Body length, 4.7 mm (range 4.33–5.00; N = 4) for females. Head, antenna and mesosoma black. Metasoma, mandibles, scape, and pedicel rufo-piceous; coxae, femora, tibiae and tarsi rufo-piceous to black in some individuals. Forewing almost entirely smoky-brown with veins dark brown.

Female. Head coriaceous, in dorsal view about 2.8-times wider than long. POL 0.9-times longer than OOL, posterior ocellus separated from inner orbit of eye by 1.67-times its longest diameter. Head in anterior view (Fig. 1A) transversely ovate, 1.48-times wider than high, moderately pubescent, with relatively long setae less abundant in frons and vertex; gena strongly broadened behind eye. Frons, face, vertex and occiput with piliferous punctures; frons with some medial rugae; facial striae radiating from clypeus reaching ventral margin of compound eye, medially absent. Clypeus 1.2-times wider than high, shiny and smooth, moderately pubescent; ventral clypeal margin convex but not projected over mandibles. Anterior tentorial pits easily visible; epistomal sulcus and clypeo-pleurostomal lines indistinct. Malar space 0.5-times the height of the compound eye. Toruli situated at mid-height of compound eye; distance between antennal rim and compound eye 0.9-times the width of antennal socket, including rim. Ocellar plate slightly raised. Occipital carina lacking. Gula short; distance between occipital and oral foramina less than height of occipital foramen (Fig. 1B). Hypostomal sulci separate at oral fossa.

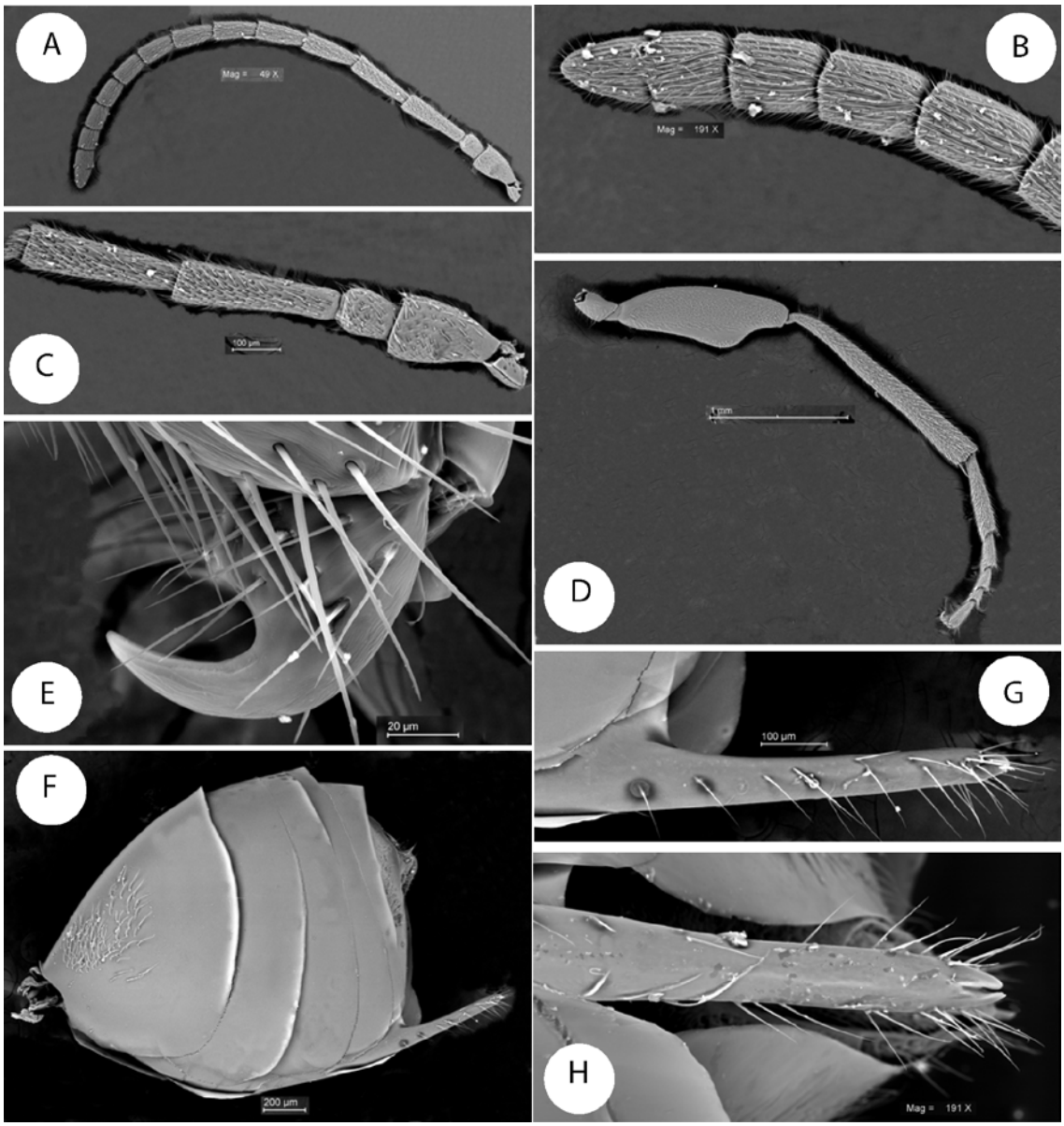

Figure 2. *Odontocynips championi*: (A) Female antenna. (B) Detail of last flagellomeres. (C) Detail of basal flagellomeres. (D) Hind leg. (E) Metatarsal claw. (F) Metasoma lateral view. (G) Spine of hypopygium lateral view. (H) Detail of ventral spine of hypopygium.

Mouthparts (Fig. 1B): mandibles strong, exposed, with long scattered setae at base; right mandible with three teeth, left with two teeth. Cardo of maxilla visible, maxillary stipes approximately 1.7-times longer than wide. Maxillary palp five-segmented. Labial palp three-segmented.

Antenna (Fig. 2 A-C) of moderate length, as long as 1/2 body length, with 14 antennomeres; flagellum not broadening towards apex, with relatively long, erect setae, and elongate placodeal sensilla visible (Fig. 2B). Relative lengths of antennal segments: 24:13:38:35:31:29:24:24:20:18:17:15:12:22. Pedicel (Fig. 2C) small, 0.5-times as long as scape; F1 1.1-times as long as F2. F6-F12 longer than wide; F12 2.2-times longer than wide, 1.8-times as long as F11 (Fig. 2B). Placodeal sensillae on F4-F12 disposed in one row of 8-10 sensillae in half-dorsal area of each flagellomere.

Mesosoma in lateral view as high as long, slightly convex dorsally.

Pronotum moderately pubescent, with relatively long setae (Fig. 1C); lateral surface of pronotum with longitudinal striae. Ratio of length of pronotum medially/laterally = 0.09. Pronotal plate indistinct dorsally (Fig. 1E).

Mesonotum (Fig. 1D) Mesoscutum coriaceous, barely pubescent, with piliferous punctures present anteriorly. Notauli complete, deep, broad and convergent posteriorly; median mesoscutal impression only indicated posteriorly. Anteroadmedian signa clearly visible. Transscutal fissure narrow, visible, not deeply impressed. Scutellar foveae ellipsoidal, shallow, approximately 1/3 as long as scutellum, smooth; internally, the foveae not clearly separated by a septum, their inner and posterior margins indistinct. Scutellum (Fig. 1D) rounded from above, approximately 0.4-times as long as mesoscutum, slightly to moderately reticulate-rugose, almost smooth anteriorly, not emarginate at posterior margin, in lateral view extending posteriorly slightly over the dorsellum. Axillula moderately pubescent, their anterior margins marked and posterior margins indistinct. Mesopleuron smooth and moderately pubescent, excepting the speculum, which is almost bare (Fig. 1C).

Metanotum (Fig. 1F): metapectal-propodeal complex: metapleural sulcus reaching posterior margin of mesopectus at approximately mid-height of metapectal-propodeal complex (Fig. 1C). Lateral propodeal carinae strong, slightly divergent posteriorly; median propodeal area longer than broad, smooth, with some setae anteriorly; lateral propodeal area densely pubescent (Fig. 1F). Nucha rugose.

Legs moderately pubescent; femora and tibiae slender; metatarsal claws simple,

with only a blunt basal lobe (Fig. 2E). Metafemur with one strong blunt lobe located in the apical third (Fig. 2D).

Forewing (Fig. 5C) as long as body; radial cell 3.3-times longer than wide, open along anterior margin; areolet ovoid, closed and distinct. R1, Rs and M nearly straight, not reaching wing margin. Rs+M reaching basalis at its mid-height. First abscissa of radius (2r) curved and 2r-m straight. Apical margin with short-hair fringe. Distal part of Cu1b vein with a short projection to the basal margin.

Metasoma (Fig. 2F) as long as head and mesosoma combined, in lateral view 1.2 time as wide as high. Second metasomal tergite covering about one-third of metasoma; anterodorsal area of second metasomal tergite with one patch of dense setae. Projecting part of hypopygial spine length (Fig. 2G), about 5-times as long as wide in ventral view, laterally with long setae, longer than spine width but not forming an apical patch (Fig. 2H).

Gall (Fig. 5 B & D). The galls are tuberous and are the largest oak galls of Panama, reaching a diameter of 45 to 100 mm. They are strongly woody, irregular, often with large aggregates of clusters of smaller galls visible, polythalamous, with rugose surface, light grayish with light green tones similar to the color of the bark when fresh (Fig. 5B) and light brown when mature (Fig. 5D). When fresh, the galls are moderately hard, but they become very hard when mature, making them very difficult to dissect. The larval cells are rounded and are in the center of the hard parenchyma (Fig. 5D). The galls are formed in stems and twigs of *Quercus bumelioides* Liebm. One species of microlepidoptera that is a borer (Fig. 5B) often emerges from the galls. The gall resembles that of *O. hansoni* Pujade-Villar, 2008, known from Costa Rica, but the latter is more regular, small and less cluster-like, the larval cells being scattered by parenchyma (Fig. 5 G-H).

Distribution. *O. championi* is a common gall found between 1500-3000 m a.s.l. at Volcan Baru, Chiriqui, Panama.

Biology. Only the asexual generation is known, inducing galls on *Quercus bumelioides* (section *Quercus*). The galls are common and can be found throughout the year in different grades of maturation on the oak branches. The old galls remain on the

trees for years. The insects studied emerged from November to January.

Taxonomic comments

Type materials from the galls collected by Champion and described as *Cynips championi* by Cameron (1883) should be housed at the NHM (London). However, after a query to that museum was made, this material could be not located (D. Notton, *pers. comm*.). Adults have never before been described. Species names based on gall descriptions before 1930 are valid, and the appropriate name for this species is *Odontocynips championi* (Cameron 1883), **comb. nov.**, but the galls found after 1930 cannot be type material. With the description above, an adult is here designated as a neotype to clarify the taxonomic position of this taxon. We further justify this nomenclatural act by the unequivocal resemblance of the gall of this species to the original, albeit somewhat short, description. Also, the collecting locality of the neotype material is the same as the original locality, and both the abundance of this gall and the common presence of a borer microlepidoptera on specimens of both collections, according to Cameron´s original description, provide additional evidence. However, adults reared from this gall collected on *Q. bumelioides* did not correspond to the genera *Andricus* or *Cynips* but more closely resembled the genus *Odontocynips*. The neotype is deposited in the Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN).

***Odontocynips hansoni* Pujade-Villar 2008**

(Figs. 3, 4 & 5 E-H)

Study material. Nine ♀ (Fig. 5E) in the Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN). PANAMA, Chiriquí, Palmira, Boquete 8º 43' 49 6" N, 82º 28' 05 7" W, 1093 m; ex., gall on stems of *Quercus lancifolia* Schledl & Cham. (Fagaceae), gall collected 23.xii.2008, insect emerged 23.xii.2008, E. Medianero leg.

Diagnosis and comments. *Odontocynips hansoni* was the first cynipid described from Costa Rica and the second species of the *Odontocynips* genus. The species was described from Cartago on *Q. insignis* (Pujade-Villar, 2008). Here, we expand the known distribution range of the species and its hosts. Furthermore, two morphological characters are added to the diagnosis of the species made in the original description as

follows: scutellum slightly emarginate at posterior margin and medially rugose; F12 1.6-times longer than wide (Fig. 3D).

Galls of *O. hansoni* are irregular, large swellings of oak stems (Fig 5G); internally there are a few scattered larval cells (Fig. 5H). They differ from the galls of *O. championi* in being more regular and much less cluster-like. Furthermore, according our sampling data in Panama, while the galls of *O. championi* are very common the galls of *O. hansoni* are rare.

Differences between the *Odontocynips hansoni* populations from Costa Rica and Panama are as follows: (i) inner margins of scutellar foveae in contact along a longer extension in Costa Rican specimens, (ii) metanotal bar smooth in Panamanian specimens and sculptured in the specimens from Costa Rica, (iii) metascutellum slightly more constricted medially in the specimens from Costa Rica, (iv) areolet slightly smaller in Costa Rican populations, and (v) the use of different hosts (*Q. lancifolia* in Panama population, *Q. insignis* in Costa Rica specimens). Despite the minor morphological features, we consider the two populations as belonging to the same species (*O. hansoni*) and highlight their differences in hopes that further studies will clarify their taxonomic positions because (i) morphologically, they are very similar in the main diagnostic characters, despite the differences mentioned; (ii) few specimens have been examined, so these differences may be intraspecific; and (iii) while the hosts are different, they are closely related because hybrids of the two species are known (http://oaks.of.the.world.free.fr/quercus_lancifolia.htm).

Key to *Odontocynips species*

1. Female antenna with 13 flagellomeres (Fig. 4B). Forewings with fuscous spots (Fig. 4H). Mesoscutum (Fig. 4C) and mesopleuron with conspicuous piliferous punctures and densely pubescent; notauli narrow. All metasomal tergites laterally pubescent (Fig. 4F). Ventral clypeal margin strongly projecting over mandibles (Fig. 4A). Lateral carinae of propodeum straight, only slightly divergent (Fig. 4D). Galls in roots. .....***O. nebulosa***

● Female antenna with 12 flagellomeres. Forewing without fuscous spots. Mesoscutum and mesopleuron with sparse pilosity and piliferous punctures; notauli broader. Only T3 laterally pubescent (Figs. 2F & 3C). Ventral clypeal margin not projected over mandibles (Figs. 1A & 3A). Lateral propodeal carinae bending posteriorly, more strongly divergent. Galls on aerial stems. **2**

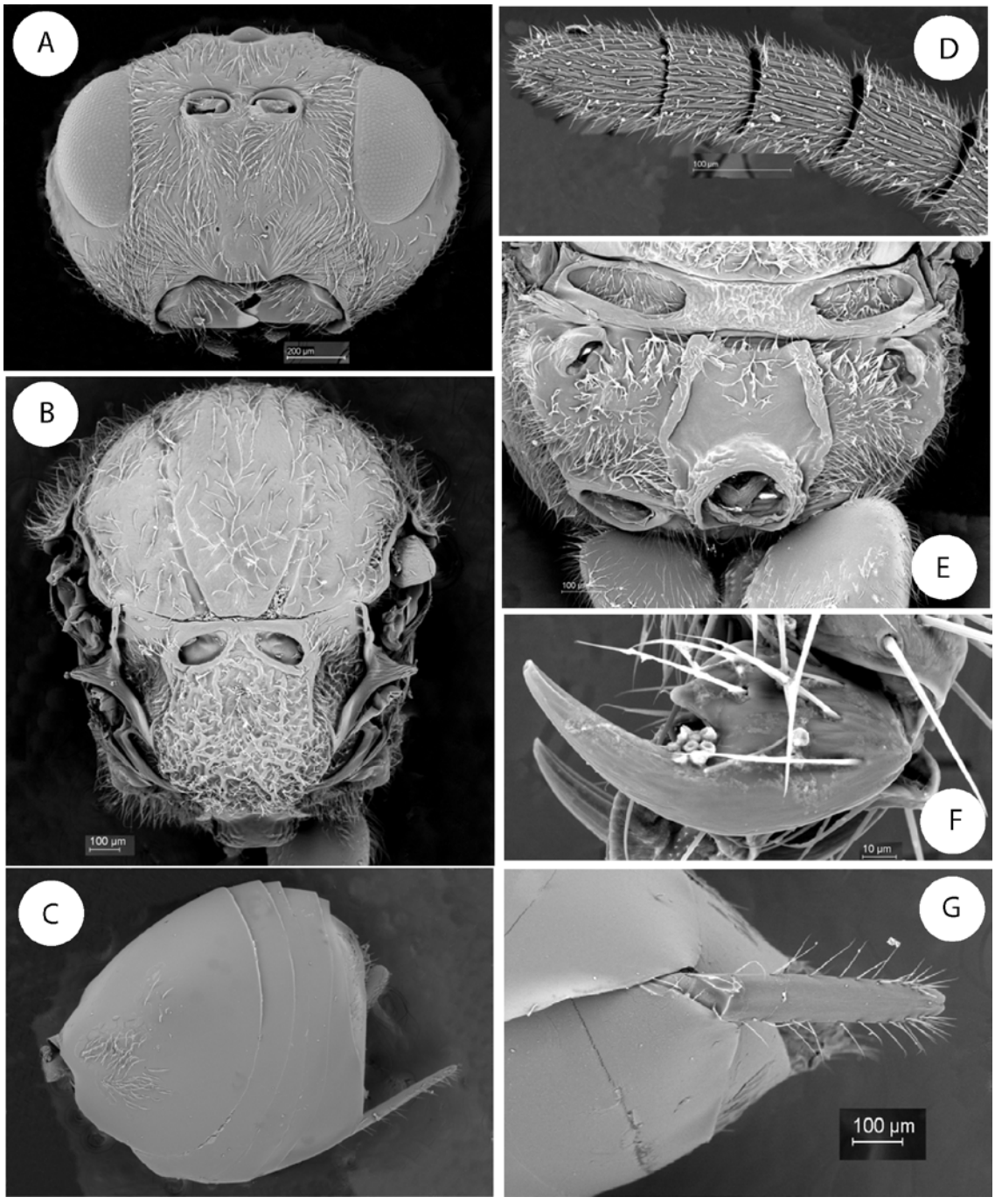

Figure 3. *Odontocynips hansoni*: (A) Head anterior view. (B) Mesosoma dorsal view. (C) Metasoma lateral view. (D) Detail of last flagellomeres, female antenna. (E) Propodeum. (E) Metatarsal claw. (G) Detail of ventral spine of hypopygium.

2. Metatarsal claw with an acute basal lobe or short tooth (Fig. 3F). Scutellar foveae with distinct margins and clearly separated (Fig. 3B); scutellar disc rugose (Fig. 3B). Median propodeal area wider than it is long; lateral propodeal carinae strongly divergent anteriorly (Fig. 3E); mesoscutum moderately pubescent (Fig. 3B). Distal part of Cu1b vein without a basal projection (Fig. 5F). ..... ***O. hansoni***

● Metatarsal claw simple, with a blunt basal lobe (Fig. 2E). Scutellar foveae with indistinct posterior and inner margins, not clearly separated by a septum (Fig. 3B). Scutellar disc almost smooth anteriorly. Median propodeal area approximately as long as wide; median propodeal carinae less divergent anteriorly (Fig. 1F); mesoscutum only slightly pubescent (Fig. 1D). Distal part of Cu1b vein with a short projection to the basal margin (Fig. 5C). ..... ***O. championi***

Discussion

The inclusion of *C. championi* within of the genus *Odontocynips* raised some doubts regarding its correct generic classification. *O. championi* Cameron and *O. hansoni* Pujade-Villar are significantly different from the type species of *Odontocynips*, *O. nebulosa,* in many morphological and biological characters (see the identification key). The three species share the presence of a large blunt lobe in the distal half of the hind femur, a character that Kieffer (1910) used to define the genus *Odontocynips*. However, because of the large differences between the species collected from Panama and Costa Rica and *O. nebulosa,* and as often occurs in Cynipini, this character could be homoplastic (Pujade-Villar, 2008). Thus, if the neotropical species belong to a different genus that also presents a lobe in the hind femur, a redefinition of the genus *Odontocynips* would be necessary, and a new genus comprising *O. championi* and *O. hansoni* could be established (Pujade-Villar, 2008). Conversely, if the large blunt lobe on the distal half of the hind femur is a true synapomorphy of the genus *Odontocynips,* the morphological variations observed in the three species, which include simple metatarsal claws (Fig. 4E), metatarsal claws simple but with a blunt basal lobe (Fig. 2E) and metatarsal claws with a short acute basal lobe (Fig. 3F), would be part of the generic variability of *Odontocynips*.

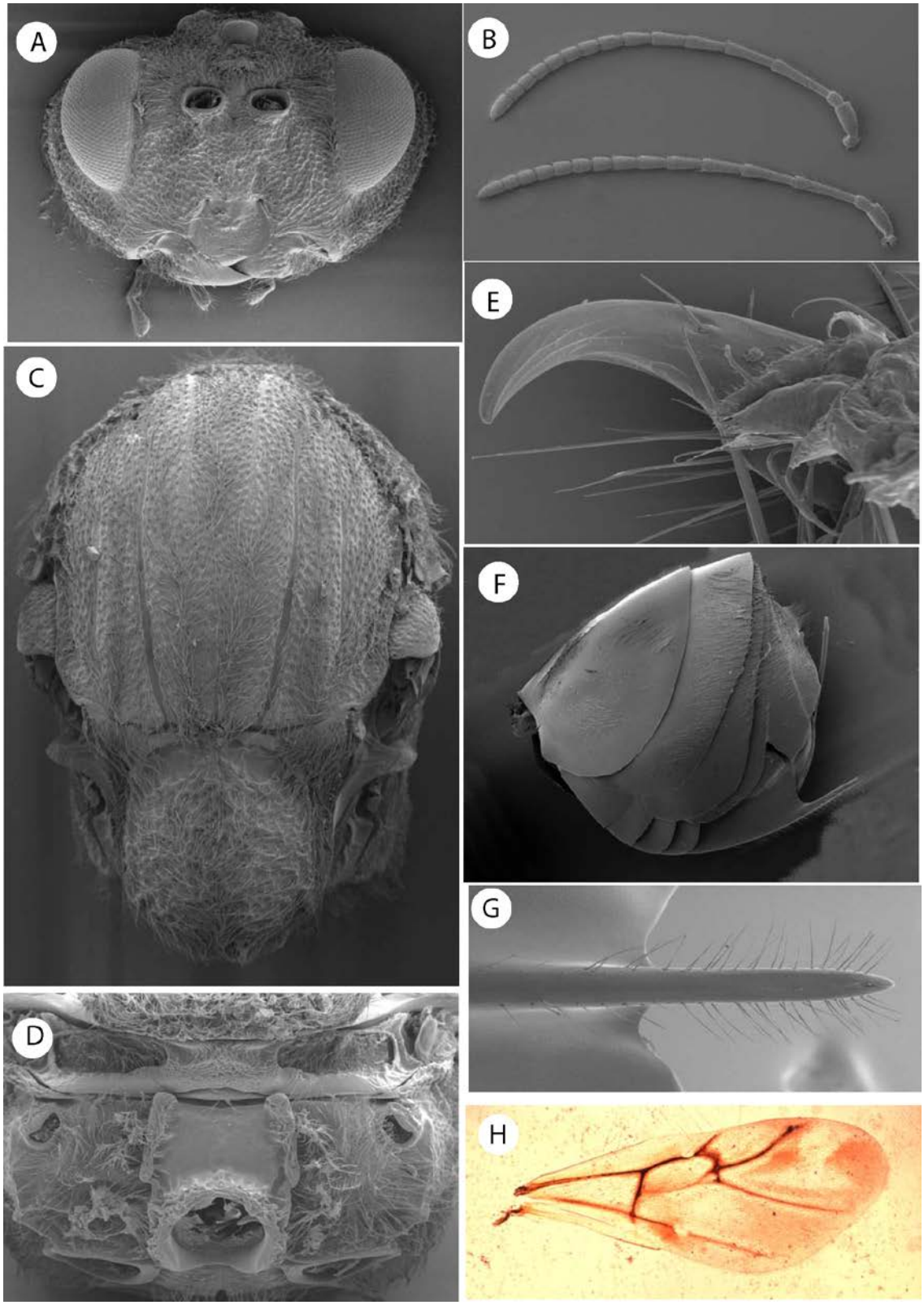

Figure 4. *Odontocynips nebulosa*: (A) Head anterior view. (B) Female antenna. (C) Mesosoma dorsal view. (D) Propodeum. (E) Metatarsal claw. (F) Metasoma lateral view. (G) Detail of ventral spine of hypopygium. (H) Forewing of female (Tomado de Liljeblad *et al.*, 2008 http://www.morphbank.net).

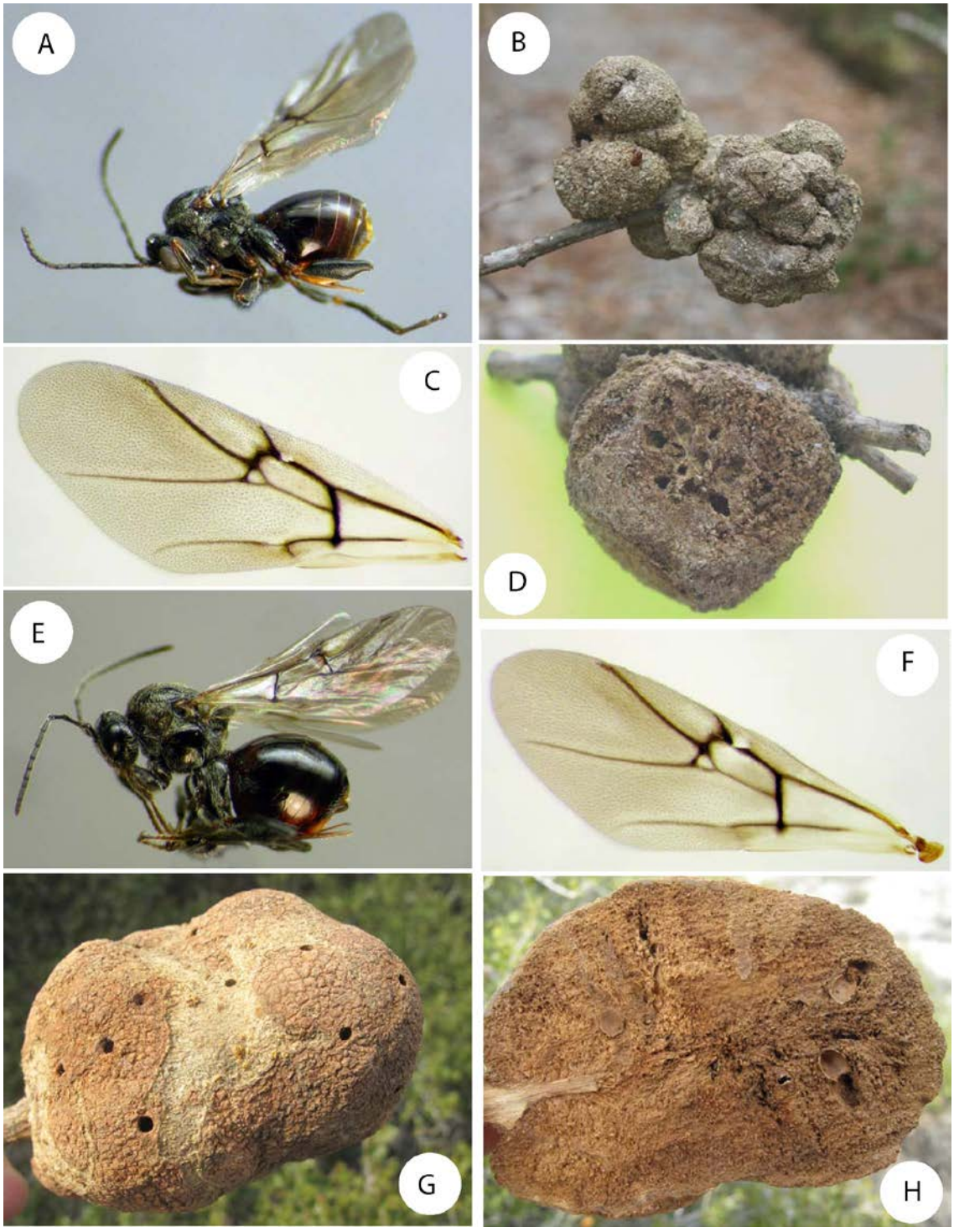

Figure 5. Habitus, forewings and galls of *Odontocynips* species: (A) *Odontocynips championi*, female (B) Mature gall of *Odontocynips championi.* (C) Forewing of female. (D) Section of a mature gall. (E) *Odontocynips hansoni*, female. (F) Forewing of female. (G) Mature gall of *Odontocynips hansoni.* (H) Section of a mature gall.

Aside from the large blunt lobe on the distal half of the hind femur, *O. championi* and *O. hansoni* resemble in most morphological characters species of *Andricus*. According to Liljeblad *et al.* (2008), *Odontocynips* is phylogenetically related to some Nearctic species of *Andricus*, especially *Andricus kingi* Bassett, 1900. We reviewed the type material of the other six species than induce woody, tuberose galls similar to the galls of *O. championi* and *O. hansoni,* and all are species of the genus *Andricus: A. tumeralis* Pujade-Villar, 2009; *A. montezumus* Beutenmüller, 1913; *A. dugesi* Beutenmüller, 1917; *A. peredurus* Kinsey, 1920; *A. furnaceus* Kinsey, 1920 and *A. durangensis* Beutenmüller, 1911. Thus, it is possible that the Central American species here studied are members of *Andricus* with a large blunt lobe on the distal half of the hind femur. Nevertheless, as the generic limits of *Andricus* are not clear, considering *Odontocynips* as part of the genus *Andricus* at this time would only further complicate the status of *Andricus* (Pujade-Villar, 2008). It is possible that the inducing of woody, tuberose, large galls is an evolutive convergence in different genera within Cynipini, as additional evidence for this conclusion is found in the literature.

It is also reasonable to think that *O. championi* and *O. hansoni* comprise a new genus taxonomically intermediate between the genera *Andricus* and *Odontocynips*. However, the main problem in the erection of a new genus including *O. championi* and *O. hansoni* is the absence of a synapomorphy that clearly defines this new taxon because these species share characters of both *Odontocynips* and *Andricus*. Consequently, we prefer be conservative and consider that the presence of a large blunt lobe on the distal half of the hind femur is a synapomorphy of the genus *Odontocynips* and that the capacity of inducing large, woody, tuberose galls is an evolutionary convergence of some species of the genera *Andricus* and *Odontocynips*. According to Pujade-Villar (2008), until the neotropical fauna of Cynipini is better known and ongoing phylogenetic analyses are finished, the erection of new genera lacking clear morphological synapomorphies is undesirable and would increase the generic chaos within Cynipini.

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CAPÍTULO 3

LOS CINÍPIDOS INQUILINOS: TRIBU SYNERGINI

OBJETIVO 3

Revisar taxonómicamente los cinípidos inquilinos de la tribu Synergini de Panamá. Describir nuevas especies y efectuar un estudio filogenético basado en la morfología externa del adulto.

3.1-*Agastoroxenia panamensis*, un nuevo género y una nueva especie de inquilino de las avispas gallícolas del roble (Hymenoptera: Cynipidae: Synergini) del Neotrópico[7]

Resumen

Se describe *Agastoroxenia panamensis* Nieves-Aldrey & Medianero, un nuevo género y una nueva especie de inquilino de las avispas gallícolas del roble (Hymenoptera: Cynipidae: Synergini), a partir de material obtenido de una agalla inducida por una especie no determinada del género *Andricus* (Cynipini) sobre *Quercus lancifolia* colectada en Panamá. El nuevo género representa el primer género de inquilinos de las avispas gallicolas de los robles descrito del Neotrópico y es la primera especie de este grupo registrada para Panamá. El nuevo género esta relacionado con *Saphonecrus* y *Synergus* pero difiere de estos géneros principalmente en la singular conformación de la antena de la hembra y del macho.

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Agastoroxenia panamensis, a new genus and species of Inquiline Oak Gallwasps (Hymenoptera: Cynipidae: Synergini) of the Neotropics

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ABSTRACT

Agastoroxenia panamensis Nieves-Aldrey & Medianero, a new genus and species of inquiline oak gallwasps (Hymenoptera: Cynipidae: Synergini), is described from material reared from unidentified *Andricus* galls (Cynipini) on *Quercus lancifolia* collected in Panama. The new genus is the first genus of inquiline oak gallwasps described from the neotropics and the first species of this group recorded from Panama. The new genus is related to *Saphonecrus* and *Synergus* but differs from these genera mainly by the unique conformation of the male and female antenna.

KEY WORDS Cynipidae, Synergini, new genus, inquilines, *Quercus*, galls, Panama.

The family Cynipidae (Hymenoptera: Cynipoidea) is a species-rich group of insects containing more than 1400 species (Nieves-Aldrey 2001; Csóka *et al* 2005; Liljeblad *et al* 2008). The majority of the cynipids, also called gall wasps, are highly specialized phytophagous insects able to induce complex galls on plants, but the family also contains representatives that inhabit plant galls induced by other insects. The great majority of this second group of gall wasps, also termed inquilines or agastoparasites (sensu Ronquist 1994), are grouped in the tribe Synergini; they inhabit galls of other cynipids and also galls induced by Cecidosid moths on *Rhus* species (van Noort *et al*. 2006). Furthermore, the known biological diversity of the Cynipidae has been recently enlarged with the discovery that the family includes also parasitoids or inquilines of

chalcid galls. A new tribe Paraulacini has been described, which include parasitoids or lethal inquilines of gall-inducing chalcids of the family Pteromalidae on Nothofagus species (Nieves-Aldrey et al. 2009).

The tribe Synergini comprises 8 genera and 170 species worldwide, but they are distributed mainly in the Holarctic Region (Nieves-Aldrey 2001; Liljeblad 2002; Melika *et al.* 2005). Four of these genera are inquiline-specific in galls on plants of the family Fagaceae, mainly on Quercus: *Ceroptres* Hartig, *Synergus* Hartig, *Saphonecrus* Dalla Torre & Kieffer, *Synophrus* Hartig, and the recently described *Ufo* Melika & Pujade Villar, which is also assigned to this biological group (Melika *et al.* 2005). *Synergus* is the most species-rich inquiline genus, with more than 90 known species distributed in the Holarctic region.

The inquiline oak Gallwasp fauna of the Neotropic have been poorly studied (Weld 1952; Ritchie and Shorthouse 1987; Nieves-Aldrey 2005; Pujade and Hanson, 2006). *Synergus filicornis* Cameron, 1883, a species described in Guatemala (Cameron 1883), was for a long time the only extant *Synergus* recorded from Central and South America. More recently, five species were added to the list: three from Guatemala: *S. cultratus* Ritchie & Shorthouse, *S. mesoamericanus* Ritchie & Shorthouse, and *S. kinseyi* Ritchie & Shorthouse (Ritchie and Shorthouse 1987); *S. nicaraguensis* Díaz & Gallardo, 1998 from Nicaragua (Díaz and Gallardo 1998); and *Synergus colombianus* Nieves-Aldrey from Colombia (Nieves-Aldrey 2005).

To date, there have been virtually no oak gall wasps species recorded south of Costa Rica. However, the distribution range of the *Quercus* host plant (section Lobatae) extends as far south as Colombia, and the genus is species-rich in Panama where nine species have been recorded (Correa *et al.* 2004). So we expected to find cynipid wasps in these countries as well. This was confirmed in recent years by cynipid wasps recorded from Colombia (Nieves-Aldrey 2005) and Panama (Nieves-Aldrey unp.; Medianero & Nieves-Aldrey unp.). The inquiline oak gallwasp fauna has been confirmed to be rich in Panama, where our preliminary studies identified more than 10 species that were all but one undescribed (Medianero & Nieves-Aldrey, in prep.). The objective of this work was to describe a new genus and species of Synergini (Cynipidae) of this fauna collected in the framework of a field study of the oak gall wasps (Cynipidae) of Panama.

Material and Methods

The studied material was collected during field surveys in Panama in 2007-2009. Fifteen specimens (10 females and 5 males), reared from galls collected in the type locality, were studied. For observation under a scanning electron microscope (SEM), adult cynipids were dissected in 70% ethanol, air dried, mounted on a stub and coated with gold, and micrographs were taken with a EVO 40 ZEISS (high vacuum technique) for several standardized views. Forewings were mounted in Euparal on slides and later examined under a Wild MZ8 stereo microscope. Images of adult habitus were taken with a NIKON Coolpix 4500 digital camera attached to a Wild MZ8 stereo microscope. Measurements were made with a calibrated micrometer scale attached to an ocular of the light microscope. Terminology of the morphological structures and abbreviations followed Ronquist and Nordlander (1989), Ronquist (1995), Nieves-Aldrey (2001) and Liljeblad et al. (2008).

Agastoroxenia Nieves-Aldrey & Medianero, **gen. n.**

(Figs. 1-3)

Type species. *Agastoroxenia panamensis* Nieves-Aldrey & Medianero, sp. n., by present designation and monotype.

Etymology. From the Greek agastoros (meaning kinsman) and xenia (meaning to seize for use) referred to the usurping of the host gall.

Description. Head (Figs. 1A, 1B, 1E). Slightly pubescent; some scattered setae on medial frons, vertex and face; some setae also dorsally on occiput and gena. Gena slightly expanded behind compound eye. Clypeus indistinct, ventral margin slightly projecting over mandibles (Fig. 1A). Anterior tentorial pits visible; epistomal sulcus and clypeo-pleurostomal lines indistinct. Face with irradiating carinae from clypeus, reaching ventral margin of eye and ventral margin of toruli; the carinae are present laterally and medially on the face; they are broad, blunt and strong; on the upper medial face the carinae are not well defined, forming an irregular rugose sculpture (Fig. 1A). Frons coriaceous, shallowly punctate. Frontal carinae present, irregular and branched near lateral ocelli. Vertex coriaceous and punctate, with some irregular rugae running from lateral ocelli (Figs. 1A, 1E). Occiput rugose dorsally. Gula relatively short (Fig. 1B); distance between occipital foramen and oral foramen not longer than the height of

the occipital foramen. Hypostomal sulci meeting at the middle part of gula (Fig. 1B). Female antenna 13-segmented (Fig. 1C); flagellum not broaden towards apex; with relatively long, erect setae and placodeal sensilla visible only on flagellar segments F8–F11. Pedicel very long, as long as scape and slightly longer than F2 (Fig. 1C). Male antenna 13-segmented (Fig. 1D). F1 dorsally curved, strongly excavated in the middle and expanded apically and basally. Placodeal sensillae present on flagellomeres 5-11.

Mesosoma. Pronotum medially relatively broad, measuring nearly 1/5 of the length of the outer lateral margin. Pronotal plate (Fig. 1F) indistinct dorsally; lateral margins of pronotum slightly angulated but without a distinct lateral pronotal carina (Figs. 1F, 2A, 2B). Notauli percurrent but slightly impressed in anterior one third (Fig. 2B). Median mesoscutal impression almost faint. Anteroadmedian signae visible. Transscutal fissure narrow. Scutellar foveae distinct. Mesopleuron with longitudinal striae and coriaceous sculpture between the striae (Fig. 2A).

Metapectal-propodeal complex. Metapleural sulcus meeting posterior margin of mesopectus at about 2/3 of height of metapectal-propodeal complex. Lateral propodeal carinae distinct, broad, subparallel but slightly curved posteriorly (Fig. 2C). Median propodeal areas smooth and pubescent. Nucha dorsally sulcate.

Legs. Metatarsal claw with a small basal acute tooth, measuring less than 1/3 of length of apical tooth (Fig. 2F).

Forewing. Radial cell closed along anterior margin, but R1 narrower and slightly depigmented along marginal cell (Fig. 3C); areolet present. Apical margin of wing with a fringe of setae.

Metasoma (Fig. 2D). T1 not completely ring shaped; sulcate, the sulci being incomplete dorsally. T2+3 covering almost the entire metasoma; smooth and shining, anteromedian area only with a row of 5-7 setae. Projecting part of hypopygial spine short (Fig. 2E); about as long as high; hypopygial spine ventrally with two rows of long setae.

Distribution. Western Panama, Chiriquí, near the border with Costa Rica.

Diagnosis and identification. The new genus is readily differentiated from other genera of Synergini by the 13-segmented antenna in both females and males. Further diagnostic antennal characteristics are the pedicel being relatively long, 2.5 times as long as wide and longer than the scape and F2, and the F1 of the male antenna being strongly curved dorsally, excavated medially, and expanded apically and basally. Other

distinctive morphological features are the small basal tooth of the metatarsal claw, measuring less than 1/3 as long as the apical tooth.

Additional diagnostic morphological features of *Agastoroxenia* are as follows: Genae expanded behind compound eyes (Fig. 1A); frontal carinae present, branched near ocelar plate and vertex; irradiating facial strigae strong, broad and blunt; ventral margin of clypeus slightly projected over mandibles; face medially with irregular longitudinal rugae; gula relatively short, distance between occipital foramen and oral foramen shorter than the height of the occipital foramen; gular sulci meeting at middle distance of gula (Fig. 1B); placodeal sensillae present in F7-10 of female antenna, arranged in one row of 2-4 sensillae; pronotum without a distinct lateral pronotal carina; notauli percurrent but faint in anterior one third of mesoscutum; mesoscutum with transverse interrupted and spaced rugae; mesopleuron longitudinally striated with coriaceous sculpture in the intervals of the striae; scutellar foveae large, the inner margins widely divergent and open posteriorly; lateral propodeal carina broad, subparallel; radial cell obsoletely closed in the margin by a depigmented R1, T2+3 covering that is 95% of the metasoma; ventral projection of hypopygium as long as high.

In the key for the identification of the world genera of Synergini (Melika et al., 2005) the new genus goes to couplet 6 and can then be distinguished as follows:

● Female and male antenna with 13 segments. Pedicel long, 2.5 as long as wide and longer than scape and F2; F1 of male antenna strongly curved dorsally, excavated medially, and expanded apically and basally. Basal tooth of the metatarsal claw small, less than 1/3 as long as apical tooth. Frontal carinae present ..... ***Agastoroxenia***

● Female antenna with 13, 14 or 15 segmented; male antenna never with 13 segments; 14, 15 or 16-segmented. Pedicel not as long; shorter than scape and F2; F1 of male less strongly curved dorsally, sometimes moderately to strongly expanded dorsally or only slightly expanded basally and apically. Basal tooth of the metatarsal claw usually larger, more than 1/3 as long as apical tooth. Frontal carinae present or not.....

.....*Synergus, Saphonecrus* and *Synophrus*

Agastoroxenia panamensis Nieves-Aldrey & Medianero sp. n.

(Figs. 1-3)

Type material. HOLOTYPE. 1♀ (in Museo Nacional de Ciencias Naturales, Madrid, Spain, card mounted. Cat., nº 2018). **PANAMA**, Chiriquí, Renacimiento, Piedra de Candela, 08º 52' 47 2" N, 82º 45' 18 2" W, 1275 m; ex gall on stems of Quercus lancifolia Schledl & Cham. (Fagaceae), gall collected 24.xi.2008, insect emerged xi.08, E. Medianero leg. PARATYPES. 4♂, 7♀ same data as holotype. Nine paratypes in MNCN, two paratypes in Maestría en Entomología, Universidad de Panamá. Additionally, 1♂, 1♀ of the type series were dissected for SEM observation.

Etymology. Named after the country where the new species was collected.

Description. Body length (measured from the anterior margin of the head to the posterior margin of the metasoma) 2.97 mm (range 2.83–3.33; N = 8) for females; 2.33 mm (range 2.00–2.58); N = 5) for males. Head, mesosoma and metasoma of female shining black, except for a rufous coloration on the lateral and basal areas of the metasoma. Antenna yellowish, with the three last flagellomeres blackish. Legs black, except for the tibiae, tarsi and apical parts of the femora, which are yellowish. Forewing hyaline, with yellowish veins. The male and female display similar coloration but the males legs are yellowish, excepting coxae.

Female. Head in dorsal view (Fig. 1E) about 2 times wider than long. Gena slightly expanded behind compound eye (Fig. 1A). POL 1.4 times longer than OOL, posterior ocellus separated from inner orbit of eye by about its longest diameter. Head in anterior view (Fig. 1A) rounded, 1.18 times wider than high, genae slightly expanded. Face with sparse setae, denser medially on the face and shorter on frons. Face with irradiating carinae from clypeus, reaching ventral margin of eye and ventral margin of toruli; the carinae are present laterally and medially on the face; they are broad, blunt and strong, but not well defined on the upper medial face, forming a irregular rugose sculpture (Fig. 1A). Clypeus indistinct, ventral margin slightly projecting over mandibles (Fig. 1A). Anterior tentorial pits visible; epistomal sulcus and clypeo-pleurostomal lines indistinct. Malar space 0.6 times height of compound eye. Toruli situated slightly below mid-height of compound eye; distance between antennal rim and compound eye 0.8 times width of antennal socket including rim.

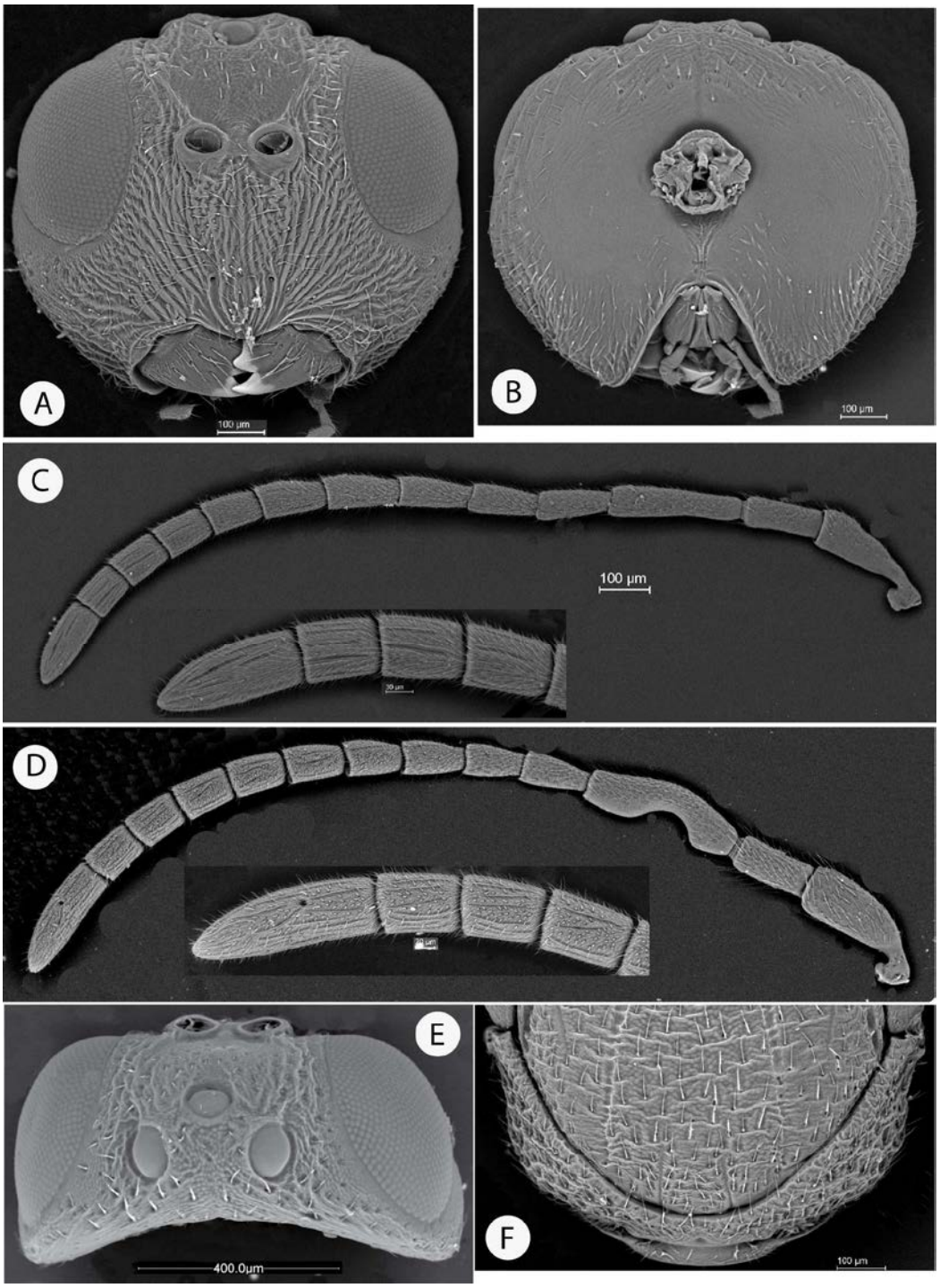

Figure 1. *Agastoroxenia panamensis* n. sp, (SEM). A, head anterior view. B, head posterior view. C, antenna female and detail of the last flagellomeres. D, antenna male and detail of the last flagellomeres. E, head dorsal view. F, pronotum anterior view.

Frons coriaceous and shallowly punctuate (Figs. 1A, 1E). Frontal carinae present, irregular and branched near lateral ocelli. Vertex coriaceous punctate, with some irregular rugae running from lateral oceli. Occiput rugose dorsally. Ocellar plate slightly raised. Gula relatively short; distance between occipital foramen and oral foramen no longer than the height of the occipital foramen. Hypostomal sulci meeting at the middle part of gula (Fig. 1B).

Mouthparts (Fig. 1B). Mandibles strong, exposed; right mandible with three teeth; left with two teeth. Cardo of maxilla visible, maxillary stipes about 1.8 times longer than wide. Maxillary palp five-segmented. Labial palp three-segmented.

Antenna 0.7 times as long as body; with 13 segments (Fig. 1C); flagellum not broadening towards apex; with relatively long, erect setae and placodeal sensilla visible only on flagellar segments F8–F11 (Fig. 1C). Relative lengths of antennal segments: 30:25:42:24:22:22:24:22:17:17:17:15:29; Pedicel long, as long as scape and slightly longer than F2; F1 1.7 times as long as F2. Ultimate flagellomere 2.6 times longer than wide, 1.9 times as long as F10. Placodeal sensillae on F8-F11 disposed in one row of 2-4 sensillae in each flagellomere.

Mesosoma. Pronotum moderately pubescent; with rugose sculpture. Ratio of length of pronotum medially/laterally = 0.3. Pronotal plate (Fig. 1F) indistinct dorsally; lateral margins of pronotum slightly angled but without a distinct lateral pronotal carina. Lateral surface of pronotum with strong rugose sculpture (fig. 2A); with sparse, white pubescence. Mesoscutum (Fig. 2B) with interrupted, sharp and widely spaced transverse carinae; the interspaces with coriaceous sculpture. Notauli percurrent although slightly impressed in anterior one third, narrow, not strongly converging posteriorly. Median mesoscutal impression almost faint, only indicated as a triangle in posterior one eighth. Anteroadmedian signa visible. Transscutal fissure narrow. Scutellar foveae distinct, 0.4 as long as scutellum, oval, smooth and rugose in part, widely separated at the inner margins and with posterior margins indistinct. Scutellum strongly rugose. Mesopleuron (Fig. 2A) with longitudinal striae and coriaceous sculpture in the interspaces.

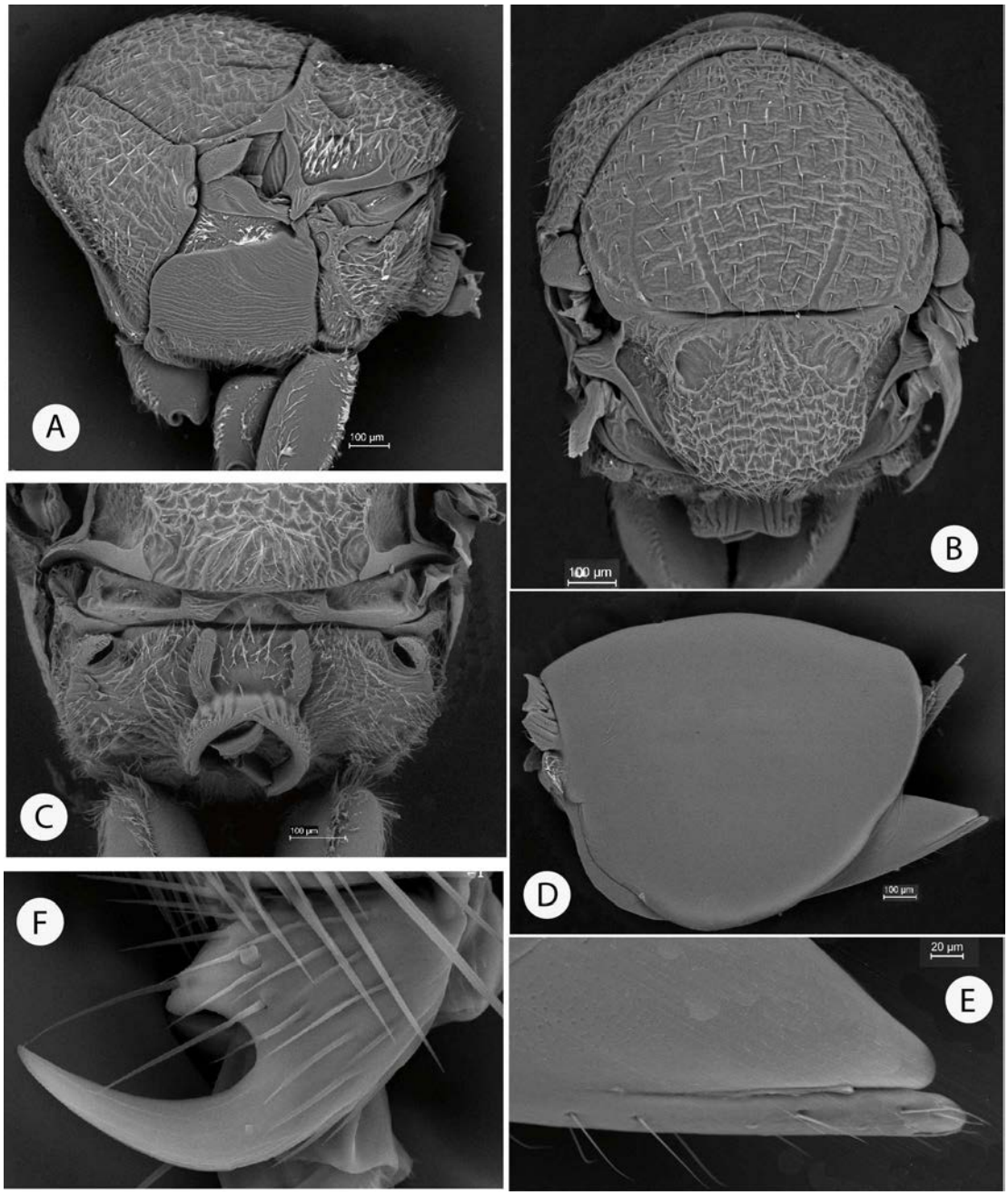

Figure 2. *Agastoroxenia panamensis* n. sp, (SEM). A, mesosoma lateral view. B, mesosoma dorsal view. C, propodeum, posterior view. D, metasoma of female lateral view. E, detail of hypopygium. F, metatarsal claw, lateral view.

Metapectal-propodeal complex. Metapleural sulcus meeting posterior margin of mesopectus at about 2/3 of height of metapectal-propodeal complex. Lateral propodeal carinae distinct, broad, subparallel but slightly curved posteriorly (Fig. 2C). Median propodeal areas smooth and pubescent. Nucha dorsally sulcate.

Legs. Tarsal claw (Fig. 2F) with base produced into a secondary acute tooth, measuring less than 1/3 of length of apical tooth.

Forewing. 0.9 as long as body. Radial cell 2.9 times longer than wide; closed along anterior margin, but R1 narrower and slightly depigmented along marginal cell (Fig. 3C); areolet present; vein Rs+M weakly pigmented, but visible, directed towards lower half of median vein. Apical margin of wing with a fringe of setae.

Metasoma (Fig. 2D). Slightly shorter than head plus mesosoma. First metasomal tergum incompletely ring-shaped, longitudinally sulcate dorsally and laterally; sulci being incomplete dorsally. Metasomal tergum T2+3 fused, smooth and shining, without micropunctures, covering almost the entire metasoma; anteromedian area only with a row of 5-7 setae. Projecting part of hypopygial spine short (Fig. 2E); about as long as high; hypopygial spine ventrally with two rows of spaced and relatively long setae.

Male. Similar to female except as follows: Antenna 13-segmented (Figs. 1D, 3B); F1 strongly excavated in the middle, expanded at base and apex and dorsally curved. Placodeal sensillae present on flagellomeres 5-11, arranged in one row of 3-5 sensillae. Relative length of antennomeres: 32:23:47:20:17:19:16:17:17:16:15:15:35. Metasoma smaller than that of female; T2 0.7 times as long as metasoma.

Distribution. The type locality is situated in the Chiriquí region of Panama, near Costa Rica, at an altitude above 1,200 m in the Cordillera of Talamanca (or Central, as it is named in Panama). The host oak, Quercus lancifolia (synonymous: *Q. corrugata* and *Q. pilarius* (Correa et al 2004), is distributed from south of Mexico to north of Panama and across all the Cordillera of Talamanca in Costa Rica, an area that represents the potential distribution of their associated gall wasp and inquilines, assuming that they are host-specific. The new genus and species is the first inquiline gall wasp taxa described from Panama. The southernmost American record for an inquiline oak gall wasp was a recently described Synergus species from Colombia (Nieves-Aldrey, 2005).

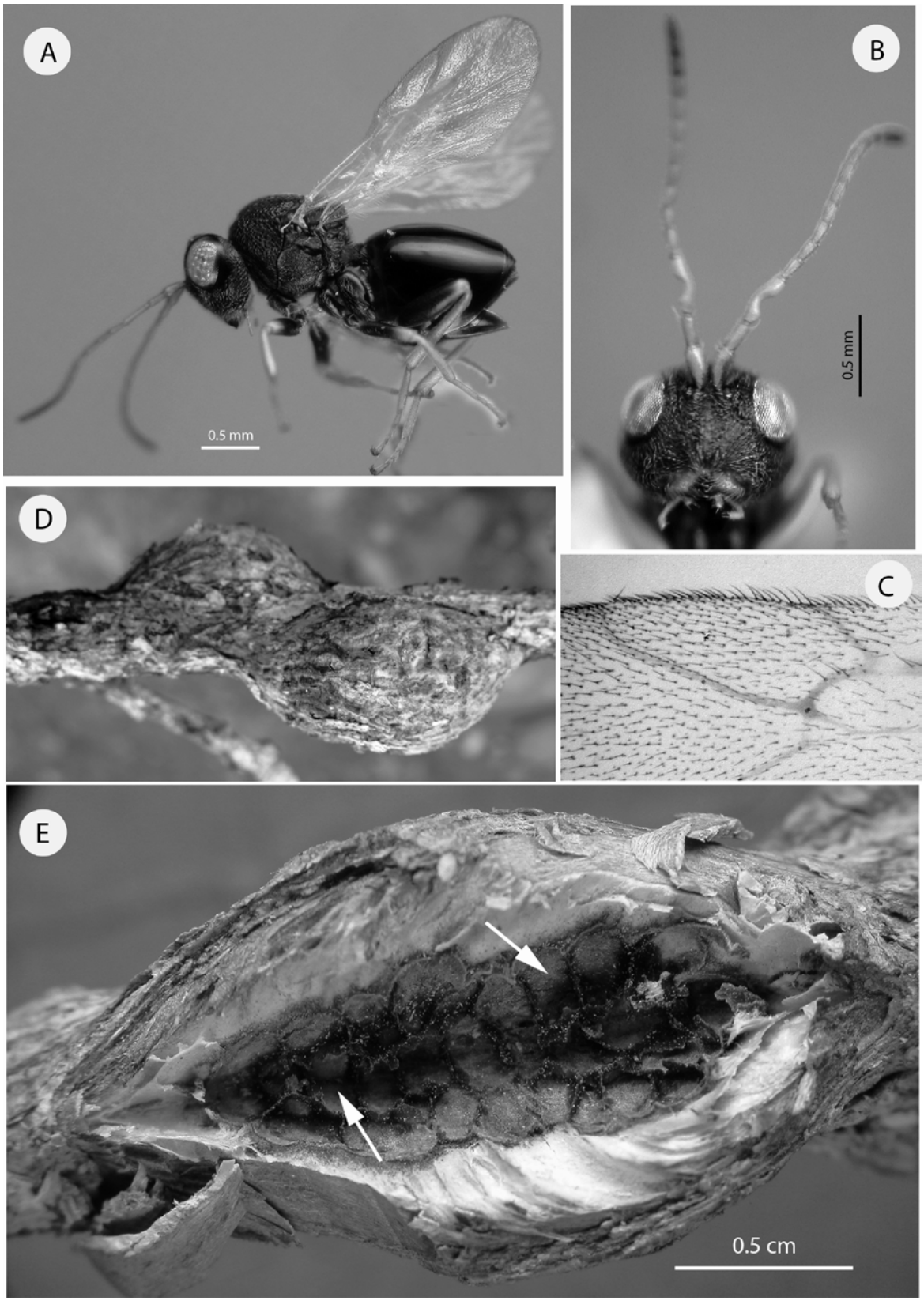

Figure 3. *Agastoroxenia panamensis* n. sp, (LM). A, adult female. B, head and antennae of the male. C, detail of the forewing. D, host gall on *Quercus lancifolia*. E, Section of a host gall showing the disposition of the inquiline larval cells (arrows pointing to individual cells).

Biology. The new species is inquiline in stem galls on *Quercus lancifolia*, induced by an unidentified *Andricus* species (Cynipidae: Cynipini). The galls (Figs. 3D, 3E) are integral, spindler shaped in the stems of the host *Quercus*. They are similar to the galls induced by *Andricus chrysolepidicola* (Ashmead, 1896) in California. The entire series of studied specimens emerged from a single gall. The host gall contained about twenty inquiline larval cells, arranged closely spaced in the centre of the gall (Fig. 3E).

Discussion

The new species here described from Panama could not being classified within any of the known described Synergini genera. In the Synergini, the number of segments of the female and male antenna is usually found to have a generic diagnostic value, and the new genus has a unique combination (13 segments in the two sexes). The erection of a new genus is justified because of this important morphological feature. Direct precedent for this description is also the recent description from Japan of *Ufo* Melika and Pujade-Villar, another inquiline genus, presumably also belonging to the group of the inquiline oak gall wasps (Melika et al. 2005), which was justified on the basis of a unique distinctive character state (the presence of a strongly impressed lateral pronotal carina, giving the pronotum a rectangular aspect in the dorsal view).

Morphologically, *Agastoroxenia* is related to *Saphonecrus* and *Synophrus*. As in these genera, the female antenna has 13 segments but the male antenna also has 13 segments, a feature unique among all the known genera of Synergini. For the slightly expanded genae, the weakly sulcate dorsal first metasomal tergum and the general sculpture of the mesoscutum and mesopleuron in the new genus resemble *Synophrus*, but the new genus has discernible frontal carinae, a character state that is shared by the majority of the *Synergus* species. The core species of *Saphonecrus* differ from *Agastoroxenia* in the absence of frontal carinae and lateral pronotal carina, but some Palaearctic species of *Saphonecrus*, such as *S. undulatus* (Mayr, 1872) resemble the new genus in having lateral pronotal carinae.

In Panama, there are at least 10 species of *Synergus* present, and most of them are undescribed (Medianero & Nieves-Aldrey in prep.). All these species have, as do the Palaearctic species of *Synergus*, 14-segmented female antennae and 15- segmented male antennae. However, unlike from the core *Synergus* Palaearctic species, all the Panamanian species, as well as the other described Neotropical species, have the

pronotum that is laterally not angulated and without a lateral pronotal carina (Nieves-Aldrey 2005; Medianero & Nieves-Aldrey in prep.). Based on this character, these species are similar to some palaeartic species of *Synergus*, such as *S. plagiotrochi* Nieves-Aldrey & Pujade, 1986 and *S. variabilis* Mayr, 1873 of the basal phylogenetic position (Ács *et al.* in press). On the other hand, the new genus *Agastoroxenia* shares with *Synergus* a closed radial cell (although the R1 is somewhat depigmented along the margin of the wing), while *Saphonecrus*, *Synophrus* and *Ufo* species all have opened radial cells.

Of the five described genera of inquilines of gallwasps associated with galls of Cynipini species on Fagaceae, *Ceroptres*, *Ufo*, *Synergus*, *Saphonecrus* and *Synophrus* (Melika et al 2005), the last three are closely related, and recent molecular evidence indicates that they belong to a monophyletic clade (Ács *et al.* in press). *Ceroptres*, the other genus of inquilines that is also linked to Fagaceae, is phylogenetically more distant (Nylander *et al.* 2004; Ács *et al.* in press).

A recent DNA barcoding study for the Palaearctic inquilines of oak gallwasps showed conclusively that morphology-based identification needs major revision at both the genus and species levels in this cynipid group (Ács *et al.* in press). The monophyly of the new genus, like that of *Ufo* and the large genus *Synergus*, including the nearctic and neotropical species, needs to be validate phylogenetically and is an obvious priority for future research. It is expected that the results of such research will provide us a more reliable morphological base for a better and stable classification of this group of cynipids.

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3.2-Taxonomía y filogenia de los inquilinos de las avispas gallicolas de los robles de Panamá, con la descripción de ocho nuevas especies de *Synergus* Hartig (Hymenoptera, Cynipidae, Synergini) [8]

Resumen

Este artículo reporta el primer estudio de los inquilinos de las avispas gallicolas de los robles de Panamá. El material proviene de muestreos realizados en 19 localidades de Panamá y las especies de inquilinos fueron recuperadas de 65 morfotipos distintos de agallas, que fueron colectadas sobre seis especies de *Quercus*, principalmente *Q. salicifolia* y *Q. bumelioides*. Se encontraron dos géneros: *Synergus* representado por 10 especies y un nuevo género para la ciencia *Agastoroxenia,* con una especie *A. panamensis*. El género *Synergus* se cita por primera vez en Panamá, así como las especies *Synergus mesoamericanus* y *Synergus nicaraguensis*, los cuales habian sido citadas para Guatemala y Nicaragua Se describen ocho nuevas especies de *Synergus*: *Synergus elegans, S. laticephalus, S. ramoni, S. rufinotaulis, S. luteus, S. gabrieli, S. baruensis y S. chiricanus*. Se aporta una clave de identificación para el material estudiado. Se efectúa un análisis filogenético preliminar de los inquilinos de las agallas de los robles, basado en caracteres morfológicos, en el que se incluyen especies del Neártico y el Paleártico como grupos externos. El análisis establece tres grupos monolofileticos bien soportados: uno en el que se incluyen las especies *Synergus elegans* y *S. laticephalus* que está cerca de *Saphonecrus lusitanicus;* otro compuesto por *Agastoroxenia* como un grupo hermano de las demás especies de *Synergus* de Panamá, que incluye la especie paleártica *S. ibericus* y un tercer clado monofilético compuesto por *S. mesoamericanus* y la nueva especie descrita *S. ramoni.*

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Taxonomy and phylogeny of inquilines of oak gall wasps of Panama, with description of eight new species of *Synergus* Hartig (Hymenoptera, Cynipidae, Synergini)

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Abstract

This paper reports the first study of the inquiline oak gall wasp fauna of Panama. Samples were collected at 19 sites in Panama, and inquiline specimens were reared from 63 gall morphotypes, including six species of *Quercus*, mainly *Q. salicifolia* and *Q. bumelioides*. Two genera were found: *Synergus*, represented by 10 species, and the newly described genus *Agastoroxenia*, with a single species, *A. panamensis*. S*ynergus* was recorded for the first time in Panama*; Synergus mesoamericanus* and *Synergus nicaraguensis*, which were formerly recorded from Guatemala and Nicaragua, have now been recorded in Panama, and eight new species of *Synergus* are described here: *Synergus elegans, S. laticephalus, S. ramoni, S. rufinotaulis, S. luteus, S. gabrieli, S. baruensis and S. chiricanus*. A key for the identification of the studied fauna is provided. A preliminary morphological phylogenetic analysis of the inquilines of oak gall wasps of Panama, including one Neotropical and two Palaearctic species as outgroups, was performed. The analysis recovered three well-supported monophyletic groups: one which is close to *Saphonecrus lusitanicus*; another composed of *Agastoroxenia* as a sister group of the core Panamanian *Synergus* species, including the Palaearctic *S. ibericus*; and a third monophyletic clade composed of *S. mesoamericanus*

and the new species *S. ramoni.*

Key words: Gall wasps, inquilines, neotropic, *Quercus*, identification key, taxonomy, phylogeny, biology.

Introduction

The inquilines (Hymenoptera, Cynipidae, Synergini) develop commensally inside the galls of other cynipids, which are a group of wasps that induce complex galls in plants, mainly in *Quercus* species (Fagaceae) (Ronquist 1994; Nieves-Aldrey 2001). Nine genera and one hundred and seventy-one species of inquilines are known, which are distributed mainly in the Holarctic region (Csóka *et al.* 2005; Melika *et al*. 2005; van Noort *et al*. 2006; Ács *et al.* 2010; Nieves-Aldrey & Medianero 2010). In the Nearctic region, eighty-nine species have been recorded (Ritchie 1984), and closer to the Centroamerican region, the fauna of Mexico is thought to be rich in inquiline species, though only two species have been actually recorded from that country (Ritchie 1984; Pujade-Villar & Melika 2005; Pujade-Villar *et al.* 2009).

The most species-rich inquiline genus is *Synergus* Hartig, with ninety-three species, which represents approximately 56% of the group's world diversity. Most *Synergus* species are distributed in the Holarctic, with forty in the Palaearctic and fifty-three species in the Nearctic. *Synergus filicornis*, a species described from Guatemala (Cameron 1883), was for a long time the only extant *Synergus* species recorded from Central and South America. In recent years, five species have been added to this list. Three of these species are from Guatemala: *S. cultratus* Ritchie & Shorthouse, *S. mesoamericanus* Ritchie & Shorthouse and *S. kinseyi* Ritchie & Shorthouse (Ritchie & Shorthouse 1987). One is from Nicaragua, *S. nicaraguensis* Díaz & Gallardo, 1998 and one species is from Colombia, *Synergus colombianus* Nieves-Aldrey, 2005 (Díaz & Gallardo 1998; Nieves-Aldrey 2005).

The gall wasp fauna of Panama, which is a small country in Central America, was almost entirely unknown with the single exception of the species *Andricus championi*, recorded from Chiriqui region (Cameron 1883). The presence of gall wasps in Panama is linked to the distribution of their host plants of the *Quercus* species, which are represented in Panama by nine species inhabiting high altitude areas in the mountains from Chiriqui to the Darien region and extending as far south as Colombia (Correa *et al*.

2004). For this reason, it has been assumed that unknown gall wasp and inquiline fauna should exist in Costa Rica, Panama and Colombia (Nieves-Aldrey 2005; Pujade-Villar & Hansson 2006). This presumption has been confirmed in recent years by the first gall wasps and inquilines being recorded from Colombia (Nieves-Aldrey 2005) and the discovery of a rich gall wasp fauna in Panama (Medianero & Nieves-Aldrey 2010; Nieves-Aldrey & Medianero 2010).

A study of the Cynipidae associated with *Quercus* species in Panama was conducted within the scope of a collaborative project of the University of Panama and the Museo Nacional de Ciencias Naturales (CSIC) (Spain). The first results of this study, including a revision of the Neotropical cynipini genus *Amphibolips*, with the description of three new species from Panama, and the description of the first inquiline from Panama, corresponding to the new genus *Agastoroxenia,* have already been published (Medianero & Nieves-Aldrey 2010; Nieves-Aldrey & Medianero 2010). Further reports on gall-inducing cynipid genera of Panama are in preparation, and we present the results concerning the inquilines here.

The objectives of the work reported here were to study the inquiline oak gall wasps of Panama taxonomically, to describe new species, to perform a preliminary phylogenetic analysis based on the morphology of the adults and to provide freshly collected specimens of the inquiline genera and species of Panama for ongoing molecular phylogenetic studies of the Synergini.

As has been revealed by recent DNA barcoding results, the present taxonomy of the inquilines of oak gall wasps is usually based on only a few diagnostic characters and a relatively poor set of morphological characters, resulting in disagreements between classifications or groupings supported by morphology and sequence data. A morphological phylogenetic analysis based on SEM images and focused on a significative group of Synergini was performed for the first time with the aim of finding a more reliable set of diagnostic characters for the Synergini.

MATERIALS AND METHODS

Selected taxa and specimens.

We studied two genera and 11 species of Synergini from Panama. All studied species were reared from cynipid galls collected from *Quercus* species at several collecting sites in Panama. The identification of the *Quercus* species was based on

several key references (Burger 1977; D'Arcy 1987; Breedlove 2001), as well as on comparison with materials from the collection of the University of Panama and the Smithsonian Tropical Research Institute.

One European species of the genus *Saphonecrus* and one European and one Neotropical species of *Synergus* were included as outgroups for comparative purposes in our phylogenetic analysis of the inquilines from Panama (Table 1).

Sampling and rearing.

Field data were taken from samplings conducted between December 2007 and May 2009 at nineteen sites in Panama. Fifteen sites in the west of Panama were sampled monthly. Intensive samplings were carried out with durations of between four to six hours per site.

Voucher specimens of all species were deposited in the entomology collections of the *Museo Nacional de Ciencias Naturales*, Madrid (Spain) and Maestría en Entomología, Universidad de Panamá (MEUP).

Unless otherwise stated, the samples were collected by the junior author of this report.

Preparation for morphological study

For observation under a scanning electron microscope (SEM), adult cynipids were dissected in 70% ethanol, air-dried, mounted on a stub and coated with gold, and micrographs were acquired with an EVO 40 ZEISS and a FEI QUANTA 200 (high vacuum technique) for several standardized views. Forewings were mounted in euparal on slides and later examined under a Wild MZ8 stereomicroscope. Images of the adult habitus were taken with a NIKON Coolpix 4500 digital camera attached to a Wild MZ8 stereomicroscope. Measurements were made with a calibrated micrometer attached to an ocular of the light microscope. The terminology used for the morphological structures and abbreviations followed Ronquist and Nordlander (1989), Ronquist (1995), Nieves-Aldrey (2001) and Liljeblad *et al*. (2008).

Phylogenetic analysis

A phylogenetic analysis was performed. The ingroup (inquilines of Panama) in the analysis was composed of *Agastoroxenia* Nieves-Aldrey & Medianero, the eight new

species of *Synergus* and *S. nicaraguensis* Diaz & Gallardo and *S. mesoamericanus* Ritchie & Shorthouse while the outgroup included *Saphonecrus lusitanicus* Tavares, 1902, *S. colombianus* Nieves-Aldrey and *S. ibericus* Tavares, 1920. Morphological variation between all of the studied inquilines was coded in an observation matrix of character states, which included coding of 65 characters, 62 of which were related to external morphology based on SEM images and three of which were based on the biology of the studied species (Table 1, Appendix I). Phylogenetic analyses were performed in PAUP* 4.0b10b (Swofford 2002). A heuristic search strategy was used to find minimum length trees using 200 random addition sequences followed by TBR-swapping (tree bisection-reconnection), with branches of maximum length zero collapsed; bootstrap analyses used the same settings but only ten random addition sequence replicates. From all parsimony searches run we considered the following models: with equal weights on all characters and no constraints.

Results

The inquilines of Panama

Agastoroxenia Nieves-Aldrey & Medianero, 2010

Diagnosis

This recently described genus is readily distinguished from other genera of Synergini by the presence of 13-segmented antenna in both females and males. Additional diagnostic antennal characteristics are the pedicel being relatively long, 2.5 times as long as wide and longer than the scape and F2, and the F1 of the male antenna is strongly curved dorsally, excavated medially and expanded apically and basally. Other distinctive morphological features are the small basal tooth of the metatarsal claw, measuring less than 1/3 as long as the apical tooth and the irradiating facial striae, which are strong, broad and blunt.

Monotypic. A single species known, *Agastoroxenia panamensis* Nieves-Aldrey & Medianero, 2010, described as an inquiline in unidentified *Andricus* galls on *Quercus lancifolia* SchIedl. & Cham. In Chiriquí, Piedra Candela (Panama) (Nieves-Aldrey & Medianero 2010)

Synergus Hartig, 1840

Diagnosis

Female antenna 14 segmented, male antenna with 15 or, rarely, 16 segments. Facial striae irradiating from the clypeus reaching the toruli and the compound eyes. Frontal carinae usually present, sometimes weak or even completely absent. Lateral pronotal carine present in most Palaearctic species, usually absent in Neotropical species. Sculpture of the mesoscutum, shape of the notauli and the scutellar foveae quite variable; lateral propodeal carinae subparallel. Radial cell of the forewing usually closed, sometimes obsoletely closed, rarely open. Metatarsal claws with a strong basal tooth, rarely simple. Metasomal terguites 2+3 usually with micropunctures on the posterior margin: sometimes inconspicuous or completely absent.

Synergus is closely related to *Saphonecrus* and S*ynophrus*, and doubts remain about the relationship between these three genera. Some basal *Synergus* species appear to be closely related to *Saphonecrus* (Acs *et al*. 2010).

Mayr (1872) divided the European *Synergus* species into sections I and II, a classification that has been followed by most subsequent authors (Tavares 1920; Eady & Quinlan 1963; Nieves-Aldrey 2001; Pujade-Villar *et al.* 2003; Melika 2006). However, recent molecular phylogenetic studies strongly indicated that this division was artificial and should not be followed, and this conclusion is also supported by the results reported here (see Discussion).

Diversity and Distribution

The world fauna of *Synergus* species were catalogued by Ritchie (1984), who listed 104 species throughout the Holarctic region. Gillette (1896) revised the 24 Nearctic *Synergus* species known at that time, and an additional 29 species have been described since (Burks 1979). Ritchie & Shorthouse (1987) revised the species from Guatemala, and new species were described from Nicaragua (Diaz & Gallardo 1998) and Colombia (Nieves-Aldrey 2005). The current estimate of the world fauna includes approximately 100 valid species.

Biology

Synergus species attack galls on *Quercus* spp., with the exceptions of *S. castanopsidis* (Beutenmueller), which is known to attack galls of *Dryocosmus*

castanopsidis on *Castanopsis* spp. in Oregon and California (Burks 1979; Pujade-Villar & Melika 2005), and an unnamed *Synergus* species from Japan that has been reared from galls of *Dryocosmus kuriphilus* Yasumatsu on the chestnut *Castanea* (Otake *et al.* 1982).

First recorded from Panama

List of species from Panama

***Synergus elegans* Nieves-Aldrey & Medianero sp. nov.**

(Figs. 1A, 3B, 5J, 6B, 8A, 10F, 13A, 15A, 16A, 17B, 18A-B)

Type material. Holotype ♀ (Fig. 18A) (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. Cat. nº 2095). PANAMA, Chiriquí, Boquete, El Salto, 8º 47' 32.08" N, 82º 27' 37.09" W, 1,431 m; ex gall *Amphibolips castroviejoi* Medianero & Nieves-Aldrey, 2010 on twigs of *Quercus salicifolia* Née (Fagaceae), gall collected 07.v.2008, E. Medianero leg. Paratypes: 3♂, 7♀, same data as holotype; 1♂, 1♀, same data as holotype, except for being collected at the road to Volcancito, 1,404 m, 31.i.2008. Ten paratypes in the MNCN, one male and one female paratype in Maestría en Entomología, Universidad de Panamá (MEUP). 1♀ paratype of the type series was dissected for SEM observation (in the MNCN).

Additional non-type material: 4♂, 8♀, ex gall *Amphibolips aliciae* Medianero & Nieves-Aldrey, 2010 on *Q. salicifolia*, Boquete, road to Volcancito, 25.i.2009; 1♀, same data, collected 12.i.2008. 1♂,7♀, ex gall *Amphibolips salicifoliae* Medianero & Nieves-Aldrey, 2010 on *Q. salicifolia*, Volcan Baru, 2,070 m, 28.i.2009; ex gall *Cynips sp*., on *Q. bumelioides*, Volcán Barú, 3,079 m, 23.x.2008. 2♂, 4♀, ex gall unidentified genus on *Q. bumelioides*, Volcán Barú, 3,079 m, 23.x.2008. 2♂, 4♀, ex gall *Disholcaspis sp*. on *Q. lancifolia*, Renacimiento, 1,270 m, 22.i.2009. 5♀, ex gall unidentified genus on *Q. bumelioides*, Volcán Barú, 1,800-2,000 m, 23.x.2008. 3♂,4♀, ex gall *Disholcaspis sp*., Volcán Barú, 1,800-2,000 m, 30.i.2008. 1♂, 4♀, ex gall of an unidentified genus on *Q. lancifolia*, Boquete, Palmira, 19.vii.2008.

Etymology. Named after the elegant, polished aspect of this wasp.

Diagnosis and comments. Together with *Synergus laticephalus* sp. n., *S. elegans* forms a distinctive group that is readily distinguished from the remaining *Synergus* species from Panama. Their main distinguishing morphological features are as follows:

head transverse-trapezoid, frontal carinae absent, horizontal sculpture of the mesopleuron not extended into the speculum, scutellum margined laterally and posterodorsally, coriarious sculpture on the mesoscutum, notauli narrow and widely separated posteriorly, scutellar foveae quadrangular and shallow; basal tooth of the metatarsal claws short, radial cell short and wide, ambiguously closed, and apical setae of the hypopigial spine extending far beyond the apex. Of the known Nearctic species, *S. elegans* resembles *S. castanopsidis* (Beutenmüller) in some characters, such as the smaller extension of the horizontal sculpture of mesopleuron (Pujade-Villar & Melika 2005), but differs in many other characters, such as the total absence of frontal carinae and the radial cell being ambiguously closed. We have also seen undescribed materials from Mexico belonging to this distinctive group.

Synergus elegans is a species that is common, highly generalist with regard to host gall preferences, and displays a high degree of morphological variability. Variation is related to its coloration, the visibility of the median mesoscutal impression, the ratio of F1/F2, and characters of the forewing venation. It remains possible that more than one cryptic species could be involved under the name *S. elegans* as here defined.

Description. Body length (measured from the anterior margin of the head to the posterior margin of the metasoma) 1.96 mm (range 1.66–2.22; N = 9) for females; 1.76 mm (range 1.34–1.90; N = 4) for males. Head predominantly yellowish or orange, frons and vertex medially, the entire occiput, clypeus medially and teeth of mandibles black; lateral areas of face and genae yellow-red. Mesosoma and metasoma of female shining black, except for a rufous coloration on the lateral and basal areas of the metasoma; tegulae yellow. Antenna and legs entirely yellowish, excepting metacoxae with brownish or blackish coloration more or less extended. Forewing hyaline, with yellow pale veins. Male with similar coloration to female but black coloration on face extended only on the ocelar triangle, and is also less extended on the metacoxae.

Female. Head in dorsal view (Fig. 3B) 2.1 times wider than long. Gena not expanded behind compound eye. POL 1.5 times longer than OOL, posterior ocellus separated from inner orbit of eye by about 2 times its diameter. Head in anterior view (Fig. 1A) wide, trapezoid, 1.4 times wider than high, genae straight, not expanded. Face weakly pubescent. Face with marked, regular, irradiating carinae from clypeus, reaching ventral margin of eye and ventral margin of toruli; the carinae are present laterally but lacking dorsomedially on the face. Clypeus indistinct, ventral margin straight, slightly

sinuate, not projecting over mandibles (Fig. 1A). Anterior tentorial pits visible; epistomal sulcus and clypeo-pleurostomal lines indistinct. Malar space 0.6 times height of compound eye. Toruli situated mid-height of compound eye; distance between antennal rim and compound eye 1.1 times width of antennal socket including rim. Frons delicately coriarious, not punctuate, without visible frontal carinae (Figs. 1A, 3B). Vertex and occiput, dorsally and laterally coriarious, without rugae or punctures. Gula relatively long; distance between occipital foramen and oral foramen slightly longer than the height of the occipital foramen. Hypostomal sulci meeting at dorsal part of gula, close to the occipital foramen.

Mouthparts (Fig. 1A). Mandibles strong, exposed; right mandible with three teeth; left with two teeth. Cardo of maxilla visible, maxillary stipes about 1.5 times longer than wide. Maxillary palp five-segmented. Labial palp three-segmented.

Antenna with 14 segments (Fig. 5J); flagellum not broadening towards apex; with relatively long, erect setae and placodeal sensilla visible on flagellar segments F6–F12. Relative lengths of antennal segments: 26:17.5:33.5:26:25:23:20.5:18:16:15.5:15:15:14:23; Pedicel 1.7 as long as wide; F1 1.3 times as long as F2. Ultimate flagellomere 2.5 times longer than wide, 1.6 times as long as F11. Placodeal sensillae on F8-F11 disposed in one single row of 2-4 visible sensillae in each flagellomere.

Mesosoma. Pronotum with sparse short pubescence. Ratio of length of pronotum medially/laterally = 0.25. Pronotal plate (Fig. 8A) indistinct dorsally; lateral margins of pronotum rounded, without a lateral pronotal carina. Lateral surface of pronotum with coriarious sculpture. Mesoscutum (Fig. 8A) with weak alutaceous-imbricate sculpture. Notauli shallowly impressed and narrow, posteriorly not wider than transscutal fissure; faint in anterior one third, not strongly converging posteriorly, widely separated at meeting with the trasscutal fissure. Median mesoscutal impression very faint or completely absent, sometimes indicated as a shallow median depression. Anteroadmedian signa virtually invisible. Scutellar foveae superficial, shallowly impressed, the shape is more or less quadrangular, their anterior margins straight and laterally forming and angle about 90° contra the transscutal fissure; posterior margins indistinct. Scutellum with alutaceous-imbricate sculpture; dorsal surface with a distinct sharp margin posteriorly and posterolaterally (Fig. 8A, 10F). Mesopleuron (Fig. 10F) with longitudinal, regular striae relatively weak, the interspaces smooth, the sculpture

not extended into the speculum (Fig. 10F).

Metapectal-propodeal complex. Metapleural sulcus meeting posterior margin of mesopectus at about 2/3 of height of metapectal-propodeal complex. Lateral propodeal carinae distinct, broad, subparallel. Median propodeal areas smooth and pubescent. Nucha dorsally sulcate.

Legs. Tarsal claw (Fig. 16A) with base produced into a secondary acute tooth relatively short, measuring less than 1/2 of length of apical tooth.

Forewing (Fig. 17B). Slightly longer than body. Radial cell 2.4 times longer than wide. R1 depigmented along marginal cell, the radial cell appearing ambiguously closed (Fig. 17B); areolet indistinct; vein Rs+M invisible. Basal cell with dense, closely spaced setae. Apical margin of wing with a moderately long fringe of setae.

Metasoma (Fig. 13A). As long as head plus mesosoma. First metasomal tergum longitudinally sulcate dorsally and laterally. Metasomal tergum T2+3 fused, smooth and shining, without micropunctures, covering almost the entire metasoma; anteromedian area only with a row of 5-7 setae. Projecting part of hypopygial spine clearly extended beyond attachment of lateral flap (Fig. 15A); lateral setae of hypopigial spine long and sparse spaced; apical setae projected beyond apex spine.

Male (Fig. 18B). Similar to female except as follows: Antenna 15-segmented; F1 weakly curvate and excavate medially, slightly expanded apically (Fig. 6B). Placodeal sensillae present on flagellomeres 2-13, arranged in one row of 2-5 sensillae. Relative length of antennomeres: 25:20:36:27:25:24:21:20:20:19:17:17:16:16:22.

Distribution. Chiriquí region of Panama, near Costa Rica, from an altitude of 1,200 m near Boquete to 3,000 m in Volcan Barú.

Biology. This new species is a generalist inquiline attacking a wide array of cynipid galls from different genera. Our data indicated that it is very common in galls of the three Panamanian species of *Amphibolips,* and it is also a frequent inquiline in galls of species of *Disholcaspis*, *Cynips* and other Panamanian cynipid genera. The host galls are detachable. The host plants of the *Quercus* section attacked by the host gall inductor belong to both the *Quercus* and *Lobata* sections.

***Synergus laticephalus* Nieves-Aldrey & Medianero sp. nov.**

(Figs. 1B, 3C, 5B, 7E, 8B, 10E, 13B, 15B, 17A, 18C)

Type material. Holotype ♀ (Fig. 18C) (in MNCN, Madrid, Spain), card-mounted.

Cat. nº 2096). PANAMA, Chiriquí, Boquete, El Salto, 8º 47' 32.08" N, 82º 27' 37.09" W, 1,431 m; ex gall of an unidentified cynipid genus on twigs of *Quercus salicifolia* Née (Fagaceae) (Fig. 22G), gall collected 19.vii.2008, E. Medianero leg. Paratypes: 4♀, same data as holotype.

Additionally, 1♀ paratype of the type series was dissected for SEM observations (in the MNCN).

Etymology. Named after the short, wide shape of its head.

Diagnosis and comments. This species is closely related to *S. elegans*, being similar in color, habitus and a majority of its morphological characters. It differs with respect to a more transverse head in dorsal view, which is more than 2.5 times as wide as long; POL about 1.2 as long as OOL and OOL more than two times the diameter of a lateral ocellus. Notauli are percurrent in *S. laticephalus*. Furthermore, F1 is as long as F2, while it is longer than F2 in *S. elegans*, and the malar distance is as long as the eye (0.6 times as long as eye in *S. elegans*).

Description. Body length 2.64 mm (range 2.53–2.77; N = 5) for females. Male unknown. Head yellow-red with frons and vertex medially and occiput black. Mesosoma black; metasoma dorsally black, and reddish ventrally; tegulae yellow. Antenna dirty yellowish; legs entirely yellowish, excepting metacoxae with reddish coloration basally. Forewing hyaline, with dirty yellow veins.

Female. Head in dorsal view (Fig. 3C) 2.7 times wider than long. Gena not expanded behind compound eye. POL 1.2 times longer than OOL, posterior ocellus separated from inner orbit of eye by 2.3 times its diameter. Head in anterior view (Fig. 1B) wide, trapezoid, 1.4 times wider than high, genae straight, not expanded. Face weakly pubescent. Face with marked, regular, irradiating carinae from clypeus, reaching ventral margin of eye and ventral margin of toruli; laterally to the toruli some rugae extended dorsally towards frons; the carinae are present laterally and medially on the face. Ventral margin of clypeus sinuate, slightly not projecting over mandibles (Fig. 1B). Malar space as long as height of compound eye. Toruli situated mid-height of compound eye; distance between antennal rim and compound eye as wide as antennal socket including rim. Frons alutaceous, not punctuate, without visible frontal carinae (Figs. 1B, 3C). Vertex and occiput without rugae or punctures. Head posterior view and mouthparts as *S. elegans.*

Antenna with 14 segments (Fig. 5B); flagellum filiform. Relative lengths of

antennal segments: 23:13:26:26:22:20:17:16:14:14:12:12:12:20; Pedicel 1.8 as long as wide; F1 as long as F2. Ultimate flagellomere 2.8 times longer than wide, 1.6 times as long as F11. Placodeal sensillae on F8-F11 disposed in one single row of 2-4 visible sensillae in each flagellomere.

Mesosoma. Pronotum with lateral margins rounded, without a lateral pronotal carina. Lateral surface of pronotum with coriarious sculpture. Mesoscutum (Fig. 8B) with weak coriarious-alutaceous-sculpture. Notauli percurrent, well impressed but narrow, posteriorly not wider than transscutal fissure; not strongly converging posteriorly, widely separated at meeting with the trasscutal fissure. Median mesoscutal impression invisible, at most indicated as an obsolete median depression. Anteroadmedian signa scarcely visible. Scutellar foveae superficial, smooth, quadrangular, posterior margins indistinct. Scutellum with coriarious sculpture and some transversal rugae visible; dorsal surface with a distinct sharp margin posteriorly and posterolaterally (Figs. 8B, 10E). Mesopleuron (Fig. 10E) with weak longitudinal, regular striae, the interspaces smooth, not extended ventrally and dorsolaterally, at the speculum (Fig. 10F).

Metapectal-propodeal complex as in *S. elegans*. Lateral propodeal carinae distinct, broad, subparallel, slightly curved.

Legs. Tarsal claw with base produced into a secondary acute tooth measuring about 1/3 of length of apical tooth.

Forewing (Fig. 17A). Slightly longer than body. Radial cell 2.4 times longer than wide. R1 depigmented along margin of radial cell, the radial cell appearing ambiguously closed (Fig. 17A); radius more heavily pigmented; areolet indistinct; vein Rs+M invisible. Basal cell with dense, closely spaced setae. Apical margin of wing with a moderately long fringe of setae.

Metasoma (Fig. 13B). As long as head plus mesosoma. First metasomal tergum longitudinally sulcate dorsally and laterally. Metasomal tergum T2+3 fused, smooth and shining, without micropunctures, covering almost the entire metasoma; anteromedian area only with a row of 5-7 setae. Projecting part of hypopygial spine not quite extended beyond attachment of lateral flap (Fig. 15B); apical setae projected beyond apex spine.

Distribution. Found at a single site near Boquete (Panama, Chiriqui), altitude 1,400 m.

Biology. This new species was reared from unidentified galls on *Quercus*

salicifolia (Quercus, Lobata section). The host gall is irregularly spherical on twigs, falling to the ground when mature (Fig. 22G). Unfortunately the gall inducer host cynipid was not reared and could not been identified, even to the generic level.

***Synergus mesoamericanus* Ritchie & Shorthouse, 1987**

New record from Panama

Studied material. 3♂, 6♀, Chiriquí, Boquete, road to Volcancito, 1,450 m, ex gall *Andricus championi* (Cameron) on *Quercus bumelioides*, 31.xii.2008. E. Medianero leg. 2♀ Volcán Barú, 2,500-3,000 m ex gall *Andricus championi* (Cameron) on *Quercus bumelioides,* 16-vi.2008.

Diagnosis and comments. As in the case of the group composed of *S. elegans* and *S. laticephalus,* this species, together with the new species *S. ramoni*, forms a clearly differentiated group, easily distinguished from the remaining *Synergus* species from Panama. Distinguishing characters include frontal carinae being indistinct, obscured by very irregular and branched interrupted rugae; facial striae irregularly sinuate, branched near the ventral margin eyes; antennae with F1 1.5 times as long as F2 in both sexes and F1 in males strongly expanded apically; basal cell of the forewing densely setose with veins being darkly pigmented and metasomal T2+3 not punctate posteriorly. The body coloration is predominantly red, red-black or black.

S. mesoamericanus was described from materials reared from large tuberose galls collected in Guatemala by Kinsey (assigned the name "*brelandi*" in their manuscript). Type material of the gall inducer insect was examined by us and corresponds to a species of *Andricus* (Nieves-Aldrey, unpublished). The galls of "*brelandi*" are, however, similar to the galls of *Andricus championi* (Cameron) from which the Panamanian material was reared.

The type material of *S. mesoamericanus* was examined by the first author (see also Nieves-Aldrey 2005). The Panamanian specimens differ from the Guatemalan specimens in their relatively larger size, longer radial cell and the R1 vein being more pigmented along the margin of the forewing, the radial cell appearing unambiguously closed, differently than previously stated in the diagnosis of the species (Ritchie & Shorthouse 1987). For this reason, we do not discard the possibility that our Panamanian specimen materials could correspond to a different closely related species. We prefer not to describe the material as new until further comparisons are made with

freshly collected materials from the type locality in Guatemala, which could elucidate this question in the future.

Additional descriptive data. Female (habitus, Fig. 18D). Head in dorsal view (Fig. 3E) 2 times as wide as long; genae not expanded behind compound eye. POL 0.9 as OOL, posterior ocellus separated from inner orbit of eye by 1.9 times its diameter. Head in anterior view (Fig. 1D) 1.2 times wider than high. Facial carinae reaching ventral margin of eye and ventral margin of toruli; dorsally extended to frons and branched near margin compound eye. Ventral margin of clypeus straight. Frons with irregular branched frontal carinae reaching ocelli, grosere piliferous punctures present (Figs 1D, 3E). Vertex and occiput without some rugae.

Female antenna with 14 segments (Fig. 5H). Pedicel 1.3 as long as wide; F1 1.5 times as long as F2. Ultimate flagellomere 1.8 times as long as F11. F1 of male curved in de middle and moderately expanded apically.

Pronotum without a lateral pronotal carina. Lateral surface of pronotum with rugose sculpture. Mesoscutum (Fig. 8E) with transverse, undulate, interrupted rugae. Notauli percurrent, convergent posteriorly and wider than transscutal fissure; narrowly separated at meeting with the trasscutal fissure. Median mesoscutal impression present, extending anteriorly about 2/3 of length of mesoscutum. Scutellar foveae ellipsoidal, anterior margins widely divergent from the trasscutal fissure, posterior margins indistinct. Scutellum not margined laterally, with rugose sculpture. Mesopleuron (Fig. 10D) with strong longitudinal, irregular striae, the striated sculpture extended into the speculum; coriarious sculpture visible in the interspaces, anterodorsally and ventrally. Lateral propodeal carinae distinct, broad, slightly convergent posteriorly.

Tarsal claw (Fig. 16D) with base produced into a secondary acute tooth measuring about 1/2 of length of apical tooth.

Forewing (Fig. 17D). Veins of radial cell well pigmented, the radial cell appearing unambiguously closed areolet distinct; vein Rs+M visible. Basal cell with dense, closely spaced setae. Apical margin of wing with a short fringe of setae.

Metasoma (Fig. 13D). Metasomal tergum T2+3 fused, smooth and shining, without micropunctures, covering almost 2/3 of metasoma; anteromedian area with a group of setae extending towards dorsal region of targeted. Projecting part of hypopygial spine quite extended beyond attachment of lateral flap (Fig. 15F); apical setae not projected beyond apex spine.

Distribution. Recorded previously from Guatemala and now from Panama (Volcán Barú).

Biology. The available biological data indicate that this species is a specialist inquiline associated with large tuberose galls induced by *Andricus* species in Panama and Guatemala (Fig. 21B).

***Synergus ramoni* Nieves-Aldrey & Medianero sp. nov.**

(Figs. **1C, 3F, 5C, 6G, 7B, 8C, 10C, 12D, 13F, 16B, 17C, 18E-F)**

Type material. Holotype ♀ (Fig. 18F) (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. Cat. nº 2097). PANAMA, Chiriquí, Boquete, El Salto, 8º 47' 32.08" N, 82º 27' 37.09" W, 1,431 m; ex gall of an unidentified cynipid genus on twigs of *Quercus salicifolia* Née (Fagaceae) (Fig. 22A), gall collected 27.xi.2008, E. Medianero leg. Paratypes: 1♂, 1♀, same data as holotype; 1♂,1♀, Boquete, Road to Volcancito, 1,404 m, 22.x.2008. E. Medianero leg. In the MNCN. Additionally, 1♀ paratype of the type series was dissected for SEM observation (in the MNCN).

Etymology. Named after Ramón Hernández, dear friend of the first author, in acknowledgment of his invaluable help in the first collecting trip of oak gall wasps of Panama, which led to this study.

Diagnosis and comments. This species is closely related to *S. mesoamericanus*, being similar in a majority of their diagnostic morphological characters. It differs from that species with respect to its black coloration, narrower head, larger ocellar triangle and the posterior ocelli being closest to the margin of eyes. Furthermore, the frons is more closely punctate, and the frontal carinae are less marked in *S. ramoni*; the sculpture of mesopleuron is weaker; the speculum is partially smooth; and the radial cell is 2.8 times as long as wide (less than 2.5 in *S. mesoamericanus*).

Description. Body length 2.75 mm (range 2.69–2.77; N = 3) for females; 2.41 (range 2.21–2.61; N = 2) for males. Head, mesosoma and metasoma predominantly black; mouthparts and sides of frons near the toruli yellowish; metasoma ventrally red brown; antennae blackish yellow; distal half less dark. Legs mainly black, apex of femora and tibiae and tarsi dark yellowish. Forewing hyaline, slightly darkened; veins brown. The male differ in having entirely the face, genae, and the antennal flagellum yellowish.

Female. Head in dorsal view (Fig. 3F) 1.9 times as wide as long. Gena not expanded behind compound eye. POL 1.6 times longer than OOL, posterior ocellus separated from inner orbit of eye by 1.3 times its diameter. Head in anterior view (Fig. 1C) narrow, only 1.1 times wider than high, genae very slightly expanded, strongly punctate. Face moderately pubescent, with marked, irregular, irradiating carinae from clypeus, reaching ventral margin of eye and ventral margin of toruli; branched near compound eyes. Ventral margin of clypeus straight not projected over mandibles. Malar space 0.6 as long as height of compound eye. Toruli situated slightly below mid-height of compound eye; distance between toruli short, shorter than diameter of a torulus; distance between mesal margin of compound eye and lateral margin of a torulus shorter than diameter of a torulus, including rim. Frons closely and conspicuously punctate, frontal carinae present but obscured by the punctate sculpture (Figs. 1C, 3F). Vertex and occiput rugose-punctate.

Female antenna with 14 segments (Fig. 5C); flagellum filiform. Relative lengths of antennal segments: 19:11:27:18:19:19:19:17:15:15:14:13:13:22; Pedicel 1.4 as long as wide; F1 1.5 as long as F2. Ultimate flagellomere 1.7 times longer as long as F11. Placodeal sensillae on F8-F11 disposed in one single row of 2-4 visible sensillae in each flagellomere. Male antenna with 15 segments; F1 excaved medially and moderately expanded apically (Fig. 6G).

Mesosoma. Pronotum without a lateral pronotal carina (Fig. 7B). Lateral surface of pronotum with rugose-punctate sculpture. Mesoscutum (Fig. 8C) with marked, undulate transverse rugae, the interspaces with coriarious sculpture. Notauli percurrent, well impressed, wider posteriorly, wider than transscutal fissure; moderately converging posteriorly. Median mesoscutal impression visible but shallowly impressed. Anteroadmedian signa well marked. Scutellar foveae ellipsoidal, with some rugose sculpture, anterior margins widely divergent from the fissure transscutal, posterior margins indistinct. Scutellum with rugose sculpture; not margined laterally and posterodorsally (Figs. 8C, 10C). Mesopleuron (Fig. 10C) medially with weak longitudinal striae, the interspaces with coriarious sculpture, the striae being weak and hardly visible dorsolaterally in the speculum (Fig. 10C).

Lateral propodeal carinae distinct, broad, subparallel. Median propodeal area pubescent, with some vertical rugae prolonged into the nucha. Nucha strongly sulcate, dorsally and laterally.

Legs. Tarsal claw (Fig. 16B) with base produced into a small secondary acute tooth measuring about 1/4 of length of apical tooth.

Forewing (Fig. 17C). Radial cell 2.8 times longer than wide. All the veins well pigmented, R1 well visible along margin of radial cell, the radial cell appearing unambiguously closed (Fig. 17C; areolet distinct; vein Rs+M visible. Basal cell with dense, closely spaced setae. Apical margin of wing with a short fringe of setae.

Metasoma (Fig. 13F). As long as head plus mesosoma. First metasomal tergum longitudinally sulcate dorsally. Metasomal tergum T2+3 fused, smooth and shining, covering almost the entire metasoma; without micropunctures; anteromedian area only with a group of about 14 setae. Projecting part of hypopygial spine slightly extended beyond attachment of lateral flap; apical setae not projected beyond apex spine.

Distribution. Known only from the type locality near Boquete and Volcán Barú (Chiriqui, Panama).

Biology. *Synergus ramoni* inhabits twig galls on *Quercus salicifolia* (*Quercus*, Lobata section). The host gall is irregularly spherical and develops on twigs (Fig. 22A). The host cynipid was not reared, and it is unknown.

***Synergus nicaraguensis* Diaz & Gallardo, 1998**

New record from Panama

Studied material. 1 ♂, 5♀, Chiriquí, Renacimiento, 1,270 m, ex gall *Disholcaspis sp.* on *Quercus lancifolia*, 24.xi.2008. E. Medianero leg.

Diagnosis and comments. This species is easily recognizable and can be distinguished from all of the remaining Neotropical *Synergus* species by having a forewing with a shaded infuscate area over the radial cell extended beyond the Rs vein. Other diagnostic features of this species are: radial cell short and wide, less than 2.5 times as long as wide. F1 3 as long as the pedicel. Metasomal T2+3 posteriorly closely and distinctly punctate, with the punctures extended over about 1/3 of the total length of the segment.

Until now, knowledge of this species was limited to the materials of the type locality (Jinotega, Nicaragua) (Diaz & Gallardo 1998). Our record from Panama is the second for this species in Central America, considerably increasing the size of its known distribution area. We examined the type material of *S. nicaraguensis* and compared it with our materials from Panama. The Panamanian insects differ slightly

from the type material in their coloration, especially with respect to their almost entirely yellow legs, which are darker in the type specimens.

Additional descriptive data. Some descriptive date and illustrations of morphological characters which were omitted in the original description are here given. Female (habitus, Fig. 19A). Head in dorsal view (Fig. 4B) 2 times as wide as long; genae not expanded behind compound eye. POL 1.5 as OOL, posterior ocellus separated from inner orbit of eye by about its diameter. Head in anterior view (Fig. 2E) 1.3 times wider than high. Facial carinae regular, deep, reaching ventral margin of eye and ventral margin of toruli; not branched near margin compound eyes. Ventral margin of clypeus straight. Frons with wide, slightly branched frontal carinae, reaching ocelli, weak piliferous punctures present.

Female antenna with 14 segments (Fig. 5E). Pedicel 1. 2 as long as wide; F1 as long as F2. Ultimate flagellomere 1.8 times as long as F11. F1 of male curved in de middle and moderately expanded apically.

Pronotum without a lateral pronotal carina. Lateral surface of pronotum with rugose sculpture. Mesoscutum (Fig. 8F) with wide, transverse, undulate, interrupted rugae, the interspaces with coriarious sculpture. Notauli percurrent, convergent posteriorly, wider than transscutal fissure; narrowly separated at meeting with the transscutal fissure. Median mesoscutal impression visible in posterior three quarts of mesoscutum but shallow. Scutellar foveae large, ellipsoidal, smooth, anterior margins widely divergent from the trasscutal fissure, posterior margins distinct. Scutellum not margined laterally, with strongly rugose sculpture. Mesopleuron (Fig. 11A) with strong, irregular, longitudinal striae, extended into the entire surface of mesopleuron; coriarious sculpture visible in the interspaces. Lateral propodeal carinae distinct, broad, subparallel (Fig. 12C).

Tarsal claw (Fig. 16C) with base produced into a large secondary acute tooth measuring about 1/2 of length of apical tooth.

Forewing (Fig. 17E). Present a shaded infuscate area over the radial cell and extended beyond the Rs vein; radial cell short and wide, less than 2.5 as long as wide; vein Rs+M visible. Basal cell with dense, closely spaced setae. Apical margin of wing with a short fringe of setae.

Metasoma (Fig. 13E). Metasomal tergum T2+3 fused, smooth and shining, with close and distinct micropunctures in posterior half of metasoma; anteromedian area with

a small group of 3-4 setae. Projecting part of hypopygial spine quite extended beyond attachment of lateral flap (Fig. 15E); hypopigial setae arranged in two rows; apical setae not projected beyond apex spine.

Distribution. Recorded from Nicaragua and now from Panama (Chiriquí, Renacimiento).

Biology. The species was originally recorded as an inquiline in an unidentified stem gall on *Quercus oleoides* that was similar to galls of *Xanthoteras quercusforticorne* (Diaz & Gallardo 1998). We have reared this inquiline from galls of an undescribed *Disholcaspis* species (Medianero & Nieves-Aldrey, unpublished). The host galls are gregarious and are formed in stems of *Quercus lancifolia* (Fig. 21H).

***Synergus rufinotaulis* Nieves-Aldrey & Medianero sp. nov.**

(Figs. 2D, 4G, 4H, 5K, 6K, 8D, 11D, 13C, 17F, 19E-F)

Type material. Holotype ♀ (Fig. 19E) (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. Cat. nº 2098). PANAMA, Chiriquí, Volcán Barú, 8º 46' 36 08" N, 82º 31' 39 03" W, 3079 m; ex gall *Cynips sp*. on twigs of *Quercus bumelioides* (Fagaceae), gall collected 23.x.2008, E. Medianero leg. Paratypes: 1♂, same data as holotype, but gall collected 22.vii.2008; 1♀, same data as holotype, reared from an unidentified gall (*Cynips* sp.?) 27.ii.2009. One paratype in the MNCN, another paratype in Maestría en Entomología, Universidad de Panamá (MEUP).

Etymology. Named after the reddish coloration of the notauli contrasting with the black mesoscutum.

Diagnosis and comments. This pretty, distinctive species differs from other Panamanian species by its long filiform antennae and long radial cell; the scutellum being subpentagonal, strongly reticulate-rugose dorsally, the large, quadrangular or irregularly rounded scutellar foveae, the wide well impressed notauli, reddish posteriorly in females, the mesopleuron with mixed striate and coriarious-rugose sculpture and the metasomal T2+3 with punctures extended about 1/3 of metasoma length. With respect to its general aspect, the micropunctate metasoma, the shape of mesoscutal sculpture and the long radial cell resembles *S. colombianus*, but these two species are well distinguished by many other characters, such as the antennal F1 of males, which is more strongly expanded in *S. colombianus*, the wider notauli of *S. rufinotaulis*, the different mesoscutal coloration, the shape of the scutellar foveae and

other features.

Description. Body length 3.36 mm (range 3.16–3.56; N = 2) for females; 2.77 (N = 1) for males.

Female. Head black excepting a narrow band along internal margin of eyes, the entire genae, the sides of the face and the bases of the mandibles which are yellowish-red or orange. Antenae brown, last flagellar segments lighter. Mesosoma black, with dorsolateral margins of pronotum, posterior one third of notauli, tegulae and dorsal margin of metascutellum orange. Metasoma black dorsally and yellowish ventrally. Legs yellow, with basal half of metacoxae black; distal half of posterior tibiae and tarsi of all legs more or less brown. Forewing hyaline, veins brown. Male differs in having the orange coloration much reduced or absent; the mesosoma being entirely black, and the metasoma almost entirely black.

Female. (Fig. 19E). Head in dorsal view (Fig. 4H) 2.2 times as wide as long. Gena not expanded behind compound eye. POL 1.2 times longer than OOL, posterior ocellus separated from inner orbit of eye by 1.5 times its diameter. Head in anterior view (Fig. 2D) trapezoid, 1.3 times wider than high, genae not expanded. Face weakly pubescent, with marked, high, strong irradiating carinae from clypeus, reaching ventral margin of eye and ventral margin of toruli; the carinae widely spaced, especially medially, the interspaces smooth. Ventral margin of clypeus straight not projected over mandibles. Malar space 0.6 as long as height of compound eye. Toruli situated at mid-height of compound eye; distance between toruli short, shorter than diameter of a torulus; distance between mesal margin of compound eye and lateral margin of a torulus shorter than diameter of a torulus, including rim. Frons with reticulate rugae, frontal carinae narrow, branched near lateral ocelli (Fig 2D). Vertex and occiput reticulate rugose, with piliferous punctures (Figs. 4G, 4H).

Female antenna with 14 segments (Fig. 5K); flagellum slender. Relative lengths of antennal segments: 18:8:27:27:25:24:20:15:14:12:11:10:9:15; pedicel slightly longer than wide; F1 as long as F2. Male antenna with 15 segments; F1 excaved medially and slightly expanded apically (Fig. 6K).

Mesosoma. Pronotum without lateral pronotal carina (Fig. 7B). Lateral surface of pronotum with reticulate-rugose sculpture. Mesoscutum (Fig. 8D) with, undulate transverse rugae, the interspaces with coriarious sculpture. Notauli percurrent, deep and wide thorough, crossed regularly by transversal mesoscutal sculpture; notauli

moderately converging posteriorly. Median mesoscutal impression visible but shallowly impressed. Anteroadmedian signa visible. Scutellar foveae rounded, smooth, anterior margins straight and not quite diverging abruptly from the fissure transscutal, posterior margins distinct. Scutellum subpentagonal, not margined, with reticulate rugose sculpture (Fig. 8D). Mesopleuron (Fig. 11D) with the horizontal striae obscured by reticulate rugae, the interspaces with coriarious sculpture.

Lateral propodeal carinae distinct, broad, slightly convergent posteriorly. Median propodeal area pubescent, not sculptured. Nucha sulcate.

Legs. Tarsal claw with secondary acute tooth measuring about 1/2 of length of apical tooth.

Forewing (Fig. 17F). As long as body. Radial cell long, 3 times longer than wide. All the veins well pigmented, R1 well visible along margin of radial cell although narrowed and less pigmented, radial cell closed (Fig. 17F; areolet indistinct; vein Rs+M visible. Basal cell with sparse spaced setae. Apical margin of wing with a moderately long fringe of setae.

Metasoma (Fig. 13C). As long as head plus mesosoma. First metasomal tergum longitudinally sulcate dorsally. Metasomal tergum T2+3 fused, covering almost the entire metasoma, smooth and shining, with well visible micropunctures, extended in posterior one third of tergite. Projecting part of hypopygial spine slightly extended beyond attachment of lateral flap; apical setae not projected beyond apex spine.

Distribution. Confined to the type locality Volcán Barú (Chiriqui, Panama).

Biology. *Synergus rufinotaulis* is present as inquiline in galls of an undescribed *Cynips* species (Fig. 22D), as well as in other detachable galls induced by an unknown cynipid species, presumably a *Cynips* species as well (Fig. 22F). In both cases, the host galls are spherical in shape, detachable and fall to the ground when mature. They grow on *Quercus bumelioides* (*Quercus*, Quercus section).

***Synergus gabrieli* Nieves-Aldrey & Medianero sp. nov.**

(Figs. 2A, 4D, 5L, 6F, 7F, 9A, 11C, 12B, 14A, 15C, 16F, 17G, 20A-B)

Type material. Holotype ♀ (Fig. 20A) (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. Cat. nº 2099). PANAMA, Chiriquí, Volcán Barú, 8º 46' 36 08" N, 82º 31' 39 03" W, 1,800-2,070 m; ex gall *Neuroterus sp*. on leaves of *Quercus bumelioides* (Fagaceae), gall collected 26.iii.2009, E. Medianero leg.

Paratypes: 6 ♂, 1♀, same data as holotype; 1 ♂, 2♀, same data but gall collected 30.i.2008. Six paratypes in the MNCN, four paratypes in Maestría en Entomología, Universidad de Panamá (MEUP).

Non-type material: 4♂, 2♀, Chiriquí, Renacimiento, 1,270 m, ex gall *Andricus guatemalensis* (Cameron) on *Quercus lancifolia*, 26.x.2008; 1♂, 1♀, same date, but gall collected at Piedra Candela, 18.vi.2008. 1♂, 2♀, Volcan Barú, ex gall *Andricus guatemalensis* on *Quercus bumelioides*, 30.i.2008. 3♂, 2♀, Boquete, Alto Quiel, 1,600 m, ex gall *Andricus guatemalensis* on *Quercus insignis*, 19.xii.2008.

Etymology. Named after Gabriel, son of the junior author.

Diagnosis and comments. A polyphagous, quite variable species; closely related to *Synergus chiricanus*, *S. baruensis* and *S. luteus*. Diagnostic characters of this species are the frontal carina being narrow and branched, faint before reaching the lateral ocelli; F1 of the female antenna 1.3 as long as F2, mesoscutum weakly coriarious with some minute closely spaced transverse rugae, metasomal T2+3 with punctures very weak, forming a narrow band.

Description. Body length 1.6 mm (range 1.50–1.66; N = 4) for females; 1.5 (range 1.19–1.58; N = 7) for males.

Female. Head yellow red, ocellar triangle, vertex medially and occiput black. Antenae yellow. Mesosoma black, excepting dorsolateral margin of pronotum yellow red and tegulae yellow. Metasoma black dorsally to brownish red posteriorly. Legs pale yellow. Forewing hyaline, veins pale yellow. Male similar coloration of female. Metasoma and forewing venation darker.

Female. (Fig. 20A). Head in dorsal view (Fig. 4D) 2.1 times as wide as long. Genae not expanded behind compound eye. POL 1.6 times longer than OOL, posterior ocellus separated from inner orbit of eye by 1.4 times its diameter. Head in anterior view (Fig. 2A) trapezoid, 1.2 times wider than high, genae not expanded behind eyes. Face weakly pubescent, with marked, high, strong irradiating carinae from clypeus, reaching ventral margin of eye and ventral margin of toruli, excepting the medial carina; the carinae are widely spaced, especially medially, the interspaces smooth. Ventral margin of clypeus weakly projected over mandibles. Malar space 0.6 as long as height of compound eye. Toruli size and relative separation as in the precedent species. Frons coriarious, weakly punctuate dorsally, frontal carinae narrow, faint before reaching lateral ocelli (Fig 4D). Vertex and occiput coriarious, with weak rugae and moderately

punctate (Figs. 2A, 4D).

Female antenna with 14 segments (Fig. 5L); flagellum slightly broadened towards apex. Relative lengths of antennal segments: 19:12:30:23:23:22:20:17:15:15:14:13:12:21; pedicel 1.5 longer than wide; F1 1.3 as long as F2. Male antenna with 15 segments; F1 slightly excaved medially and very weakly expanded basally and apically (Fig. 6F).

Mesosoma. Pronotum without lateral pronotal carina (Fig. 7B). Lateral surface of pronotum with weakly-rugose sculpture. Mesoscutum (Fig. 9A) with, very weak interrupted transverse rugae, the interspaces with coriarious sculpture. Notauli percurrent, narrow and moderately converging posteriorly, with of a notaulus posteriorly not as wide as transscutal fissure. Median mesoscutal impression not visible. Scutellar foveae ellipsoidal, smooth, anterior margins moderately diverging from the fissure transscutal, posterior margins discernible. Scutellum not margined, with moderate rugose sculpture, weaker medially (Fig. 9A). Mesopleuron (Fig. 11C) with regular horizontal striae extended on the speculum, the interspaces smooth, coriarious sculpture not apparent.

Lateral propodeal carinae distinct, broad, slightly convergent posteriorly (Fig. 12B). Median propodeal area smooth, with short pubescence. Nucha sulcate.

Legs. Tarsal claw with secondary acute tooth measuring about 1/3 of length of apical tooth (Fig. 16F).

Forewing (Fig. 17G) longer than body. Radial cell long, 3.4 times longer than wide. R1 not well visible along margin of radial cell, narrowed and less pigmented, radial cell ambiguously closed; areolet indistinct; vein Rs+M invisible. Basal cell with widely spaced sparse setae. Apical margin of wing with a long fringe of setae.

Metasoma (Fig. 14A). First metasomal tergum longitudinally sulcate dorsally. Metasomal tergum T2+3 fused, covering 4/5 parts of metasoma, smooth and shining, with minute, obsolete, micropunctures forming a narrow band posterodorsal to tergite. Anterolateral pubescence composed of a group of 4-5 setae. Projecting part of hypopygial spine slightly extended beyond attachment of lateral flap; apical setae not projected beyond apex spine (Fig. 15C).

Variation. *S. gabrieli* is a relatively common species that inhabits a moderately wide array of host cynipid galls. The variability of this species is accordingly high. Its variability is related not only to its coloration but also to the sculpture of the frons,

vertex and mesoscutum, the relative average of antennal F1 and F2 and the shape of F1 of the male antennae. It is possibile that that this variability may obscure the existence the some closely related cryptic species. Ongoing molecular DNA studies may answer this question in the future.

Distribution. Chiriqui region, Panama.

Biology. This new species is a polyphagous inquiline that shows a preference for attacking the leaf galls induced by *Andricus guatemalensis* (Fig. 21D) and an undescribed species of *Neuroterus* (Fig. 21E) on *Quercus* species of both the *Quercus* and *Lobatae* sections.

Synergus chiricanus **Nieves-Aldrey & Medianero sp. nov.**

(Figs. 2B, 4C, 5I, 6D, 7D, 9D, 11B, 12A, 14B, 17H, 20C)

Type material. Holotype ♀ (Fig. 20C) (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. Cat. nº 2100). PANAMA, Chiriquí, Boquete, Bajo Mono 8º 49' 44 06" N, 82º 28' 37 01" W, 1,547 m; ex gall *Andricus* sp. on buds of *Quercus insignis* (Fagaceae), gall collected 26.i.2009, E. Medianero leg. Paratypes: 1♂, 2♀, same data as holotype. Two paratypes in the MNCN, one paratype in Maestría en Entomología, Universidad de Panamá (MEUP).

1♀ paratype of the type series was dissected for SEM observations (in the MNCN).

Etymology. Named after the region of the collecting site.

Diagnosis and comments. This species is morphologically similar to the closely related species S. *gabrieli*, S. *baruensis* and *S. luteus*. It differs from these species, in addition to its smaller size, with respect to the mesoscutal sculpture, which is strong, with the interrupted transverse rugae widely spaced; F1 of female antenna 1.9 as long as pedicel; 1.1 as long as F2, septum separating the scutellar foveae being broad and the lateral propodeal carinae strongly convergent. The radial cell is less than three times as long as wide.

Description. Body length 1.86 mm (range 1.82–1.90; N = 2) for females; 1.98 (N = 1) for males.

Female. Head yellow red, excepting the frons and the occiput medially black. Antenae dirty yellow, brownish apically. Mesosoma black, excepting dorsolateral margin of pronotum reddish and tegulae yellow. Metasoma black dorsally to brownish red posteriorly. Legs yellow. Forewing hyaline, veins pale yellow. Male similar

coloration of female but lateral surface of pronotum yellow, dorsal areas of mesopleuron reddish, distal areas of metasoma yellow reddish.

Female. (Fig. 20C). Head in dorsal view (Fig. 4C) about 2 times as wide as long. Genae slightly expanded behind compound eye. POL 1.4 times OOL, posterior ocellus separated from inner orbit of eye by 1.2 times its diameter. Head in anterior view (Fig. 2B) rounded, 1.2 times wider than high, genae slightly expanded behind eyes. Sculpture on face similar to *S. gabrieli*. Malar space 0.5 as long as height of compound eye. Toruli size and relative separation as in the precedent species. Sculpture on frons and vertex similar as *S. gabrieli*. (Figs. 2B,4C).

Female antenna with 14 segments (Fig. 5I); flagellum slightly broadened towards apex; pedicel 1.2 as long as wide; F1 1.2 as long as F2. Male antenna with 15 segments; distal half widened. F1 excaved medially and slightly expanded apically (Fig. 6D).

Mesosoma. Pronotum without lateral pronotal carina (Fig. 7D). Lateral surface of pronotum with coriarious-striated sculpture. Mesoscutum (Fig. 9D) with, strong, interrupted transverse carinae, the interspaces with coriarious sculpture. Notauli percurrent, narrow and moderately converging posteriorly, width of a notaulus posteriorly as wide as transscutal fissure. Median mesoscutal impression not visible. Scutellar foveae ellipsoidal, smooth, widely separated anteriorly by a septum; anterior margins diverging from the fissure transscutal, posterior margins visible. Scutellum not margined, with moderate rugose carinate sculpture, (Fig. 9D). Mesopleuron (Fig. 11B) with wide, blunt, close spaced horizontal striae, extended on the speculum, the interspaces without visible coriarious sculpture.

Lateral propodeal carinae distinct, broad, strongly convergent posteriorly (Fig. 12A). Median propodeal area smooth and pubescenct. Nucha sulcate.

Legs. Tarsal claw with secondary acute tooth large, measuring about 1/2 of length of apical tooth.

Forewing (Fig. 17H). Radial cell 3 times as long as wide. R1 depigmented along margin of radial cell, radial cell ambiguously closed; areolet indistinct; vein Rs+M invisible. Basal cell with widely spaced sparse setae. Apical margin of wing with a long fringe of setae.

Metasoma (Fig. 14B). First metasomal tergum longitudinally sulcate dorsally. Metasomal tergum T2+3 fused, covering 4/5 parts of metasoma, smooth and shining, micropunctures absent. Anterolateral pubescence composed of a group of 4-5 setae.

Hypopygial spine as in *S. gabrieli*.

Distribution. Chiriqui region, Panama.

Biology. Reared only from small galls within buds of *Quercus insignis*. The cynipid host is an unidentified *Andricus* species that is likely undescribed.

***Synergus baruensis* Nieves-Aldrey & Medianero sp. nov.**

(Figs. 2C, 4F, 5F, 6J, 9C, 11F, 14C, 17J, 20D-E)

Type material. Holotype ♀ (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. (Cat. nº 2101). PANAMA, Chiriquí, Boquete, Alto Chiquero 8º 50' 49 01" N, 82º 29' 18 04" W, 1869 m; ex gall of an undescribed *Callirhytis*? species on *Quercus salicifolia* (Fagaceae), gall collected 10.v.2008, Medianero & Nieves leg. Paratypes: 6♂, 6♀, same data as holotype; 1♂, road to Volcancito, 1,400 m, 25.i.2009, E. Medianero leg. Eight paratypes in the MNCN, four paratypes in Maestría en Entomología, Universidad de Panamá (MEUP).

1♀ paratype of the type series was dissected for SEM observations (in the MNCN).

Etymology. Named after the Volcan Barú, the best collecting site for cynipids in Panama.

Diagnosis and comments. This new species resembles *S. luteus*, *S. gabrieli* and *S. colombianus* in its general aspect and in most morphological characters. The distinguishing characters for these species are mentioned in the identification key. The diagnostic characters of *S. baruensis* can be summarized as follows: coloration predominantly yellowish in the two sexes; frontal carinae strong, high, not branched, reaching close to the lateral ocelli; F1 of female antenna 2.8 as long as pedicel; 1.2 as long as F2; sculpture of mesoscutum weakly coriarious with some weak transverse rugae; lateral propodeal carinae moderately convergent; radial cell three times as long as wide, venation well pigmented, in males the distal end of the radial cell is extended by a pigmented small triangle; extension of micropunctures on the posterior metasomal 2+3 terguites forming a narrow band, punctures quite weak

Description. Body length 2.4 mm (range 2.14–2.77; N = 6) for females; 2.4 (range 1.82–2.85; N = 7) for males.

Female (Fig. 20D). Head yellow red, the frons (inside frontal carinae), ocelar triangle and occiput, around the occipital foramen, black. Antennae brown dorsally and yellowish ventrally. Mesosoma black, but sides of pronotum and scutellum, lateral

margins of mesoscutum and speculum are yellow red; tegulae yellow. Metasoma black dorsally and anterolaterally, the half ventral and the posterolateral areas yellow. Legs yellow, excepting all tarsi slightly darkened. Forewing hyaline, veins dirty yellow. Male (Fig. 20E) similar to female but yellow coloration much more extended, only small areas black in pronotum medially, sides of ocelli, posterior half of mesoscutum (among notauli), propodeum and metasoma dorsally. Coxae of legs more pale yellow.

Female. (Fig. 20D). Head in dorsal view (Fig. 4F) 2 times as wide as long. Genae not expanded behind compound eye. POL 1.8 times OOL, posterior ocellus separated from inner orbit of eye by about its diameter. Head in anterior view (Fig. 2C) more or less trapezoid, 1.2 times as wide as high, genae slightly expanded behind eyes. Facial carinae strong, regular, reaching toruli and internal margin of eyes, not branched near compound eyes. Malar space 0.5 as long as height of compound eye. Toruli size and relative separation as in their closely allied species. Frontal carinae strong, high, not branched, close arriving lateral ocelli. Frons coriarious, with some punctures and very weak rugae; vertex and dorsal area of occiput coriarious punctuate; some rugae close to internal margins of eyes (Figs. 2C, 4F).

Female antenna with 14 segments (Fig. 5F); flagellum filiform not broadened towards apex; relative lengths of antennal segments: 18:9.5:28:23:21:21:18.5:16:13:12:11:10:10:18.5; pedicel 1.3 as long as wide; F1 1.2 as long as F2. Male antenna with 15 segments; distal half slighty broadened; F1 excaved medially and slightly expanded apically (Fig. 6J).

Mesosoma. Pronotum without lateral pronotal carina. Mesoscutum moderately pubescent (Fig. 9C); with weak, coriarious striate sculpture. Notauli percurrent, narrow and moderately converging posteriorly; notauli not broadened posteriorly, as wide as transscutal fissure. Median mesoscutal impression virtually invisible. Scutellar foveae ellipsoidal, shallow, smooth, narrowly separated anteriorly by a septum. Scutellum not margined, with rugose sculpture. Mesopleuron (Fig. 11F) with close spaced horizontal striae, extended on the speculum, the interspaces without visible coriarious sculpture. Lateral propodeal carinae distinct, broad, moderately convergent posteriorly (Fig. 12A). Median propodeal area smooth and pubescenct. Nucha sulcate.

Legs. Tarsal claw with secondary acute tooth large, measuring about 1/2 of length of apical tooth.

Forewing (Fig. 17J). Radial cell 2.9 times as long as wide. R1 slightly narrower

along margin of radial cell, but radial cell closed; areolet indistinct; vein Rs+M incomplete. Basal cell with few sparse setae. Apical margin of wing with a long fringe of setae.

Metasoma (Fig. 14C). First metasomal tergum longitudinally sulcate dorsally. Metasomal tergum T2+3 fused, covering 4/5 parts of metasoma, smooth and shining, weak micropunctures visible forming a narrow band on posterodorsal area of terguite. Anterolateral pubescence forming a patch of about 14 setae. Projection of the hypopygial spine short; apical setae not projected beyond apex spine.

Distribution. Chiriqui region, Panama.

Biology. *Synergus baruensis* is an inquiline inhabiting galls of an undescribed cynipid species that are provisionally attributed here to the genus *Callirhytis*. The galls are grown on the leaves and buds of *Quercus salicifolia*, being integral and plurilocular (Fig. 21G). Both the host galls and the inquiline cynipid seem to be common in the Chiriquí region of Panama.

Synergus luteus **Nieves-Aldrey & Medianero sp. nov.**

(Figs. 2F, 4E, 5G, 6E, 9B, 11E, 14D, 15D, 16E, 17I, 20F-G)

Type material. Holotype ♀ (in Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), card-mounted. Cat. nº 2102). PANAMA, Chiriquí, Volcan Barú , Rio Seco 8º 47' 54 05" N, 82º 30' 32 05" W, 2447 m; ex gall of *Loxaulus sp* on *Quercus bumelioides* (Fagaceae), gall collected 26.xi.2008, E. Medianero leg. Paratypes: 2♂, 5♀, same data as holotype; 1♂, 1♀, same data as holotype, but collected at 2,870 m, 22.xii.2008. Seven paratypes in the MNCN, two paratypes in Maestría en Entomología, Universidad de Panamá (MEUP).

1♀ paratype of the type series was dissected for SEM observations (in the MNCN).

Etymology. Named after the predominantly yellow coloration of this species.

Diagnosis and comments. Closely related to *Synergus colombianus* and *Synergus baruensis*; can be distinguished from *S. colombianus* by the F1 being longer than F2 in the female antenna and not strongly expanded dorsally in male antenna, in addition to its predominantly yellow coloration. Compared to *S. baruensis*, *S. luteus* differs in its coloration, in the weaker and more branched frontal carinae, the stronger transverse sculpture of the mesoscutum, the expanded genae and the metasomal 2+3 terguites

being visibly punctate posteriorly.

Description. Body 2.7 mm (range 2.45–3; N = 5) for females; 2.05 (range 1.9–2.2; N = 2) for males.

Female (Fig. 20F). Head yellow red, the ocelar triangle, the occiput, around the occipital foramen, and tip of mandibles black. Antennae yellow. Mesosoma predominantly yellow red; the margin anterolateral of pronotum, anterior part of anteromedial signa, ventral area of mesopleuron, metanotum and propodeum black. Metasoma yellowish red, dorsally black. Legs yellow, excepting the metatarsomeres slightly darkened. Forewing hyaline, veins pale yellow. Male (Fig. 20G) similar to female but black coloration more extended on frons and vertex medially, the entire mesonotum and the metasoma, excepting its apical area.

Female. (Fig. 20F). Head in dorsal view (Fig. 4E) 2 times as wide as long. POL 1.3 times OOL, posterior ocellus separated from inner orbit of eye by 1.3 times its diameter. Head in anterior view (Fig. 2F) more or less rounded, 1.2 times as wide as high, genae slightly expanded behind eyes. Facial carinae strong, regular, reaching toruli and internal margin of eyes, slightly branched near compound eyes, medially in face the carinae arriving close to ventral margin of toruli. Ventral margin of clypeus slightly projected over mandibles. Malar space 0.6 as long as height of compound eye. Toruli size and relative separation as in their closely allied species. Frontal carinae branched and diffuse close lateral ocelli. Frons coriarious-punctate; vertex and dorsal area of occiput coriarious-punctate (Figs. 2F, 4E).

Female antenna with 14 segments (Fig. 5G); flagellum filiform not broadened towards apex; relative lengths of antennal segments: 20:11:29:22:23:24:21:20:16:15:15:12:12:24; pedicel 1.3 as long as wide; F1 1.3 as long as F2. Male antenna with 15 segments; distal half slighty broadened; F1 curvated medially and slightly expanded apically; F1 2 times as long as F2 (Fig. 6E).

Mesosoma. Pronotum without lateral pronotal carina, laterally with coriarious-striate sculpture. Mesoscutum moderately pubescent, with strong horizontal, closely spaced, striate sculpture (Fig. 9B). Notauli percurrent, slightly converging posteriorly; notauli slightly broadened posteriorly, being wider than width of transscutal fissure. Median mesoscutal impression not impressed. Scutellar foveae ellipsoidal, shallow, slightly rugose, separated anteriorly by a narrow septum. Scutellum not margined, with horizontal, irregular, rugose sculpture. Mesopleuron (Fig. 11E) with close spaced,

regular, horizontal striae, extended also on the speculum, the interspaces without visible coriarious sculpture.

Lateral propodeal carinae distinct, broad, rather convergent posteriorly. Median propodeal area smooth and pubescenct. Nucha sulcate.

Legs. Tarsal claw with secondary acute tooth large, measuring 1/2 of length of apical tooth (Fig. 16E).

Forewing (Fig. 17I). Radial cell long, about 3.2 times as long as wide. R1 slightly depigmented along margin of radial cell, the radial cell appearing ambiguously closed; areolet inconspicuous but visible; vein Rs+M quite pale, but visible. Basal cell sparsely pubescent. Apical margin of wing with a long fringe of setae.

Metasoma (Fig. 14D). First metasomal tergum longitudinally sulcate dorsally. Metasomal tergum T2+3 fused, covering almost all the metasoma, smooth and shining, micropunctures present, forming a band on posterior one third of metasomal terguite. Anterolateral pubescence forming a group of about 7 setae. Projecting part of the hypopygial spine clearly expanded beyond attachment with sternite (Figs. 14D, 15D); lateral pubescence of hipopigial spine conspicuous and closely spaced; apical setae of hypopigial spine not projecting beyond apex spine.

Distribution. Known from the Volcán Barú area, Chiriqui region, Panama.

Biology. This new species inhabits galls of an undescribed species of the *Loxaulus* or *Bassettia* genera (Medianero & Nieves-Aldrey in prep.). The host galls consist of small swellings, which are sometimes inconspicuous, on twigs or small branches of *Quercus bumelioides.* The host galls are, thus, integral non-detachable, plurilocular and often cryptic (Fig. 22B).

Key to inquiline species of Panama

1 Female and male antenna with 13 segments. Pedicel long, 2.5 as long as wide and longer than the scape and F2 (Fig. 5A); F1 of male antenna strongly curved dorsally, excavated medially, and expanded apically and basally (Fig. 6A). Basal tooth of the metatarsal claw small, less than 1/3 as long as the apical tooth. Frontal carinae present (Fig. 1F) ..... ***Agastoroxenia***

● Female antenna with 14 segments, rarely 15; male antenna 15 segmented. Pedicel not as long; being shorter than the scape and F2 (Figs 5B-L); F1 of males less strongly curved dorsally, sometimes moderately to strongly expanded dorsally, or only slightly expanded basally and apically (Figs. 6B-K). Basal tooth of the metatarsal claw usually more than 1/3 as long as apical tooth. Frontal carinae present or absent (Figs 1A, 2C) ..... 2 (**Synergus)**

2 Mesopleuron with longitudinal, horizontal striate sculpture extended only medially and basally, speculum of mesopleuron smooth and shining; the striae weak (Figs. 10E, 10F). Scutellum with a clear and projected posterior margin, also margined laterally (Figs. 8B, 10F). Scutellar foveae shallow, sometimes indistinct (Fig. 8A). Notauli narrow, widely separated posteriorly (Fig. 8A). Subapical setae of the ventral spine of the hypopygium long, projected beyond the apex spine (Fig. 15A). Frontal carina absent; front and vertex with coriarious sculpture, not punctuate (Fig. 1A). Metasomal tergum T2+3 without micropunctures posteriorly (Fig. 13A) **3**

● Mesopleuron entirely striate, the striae usually stronger and extended on the speculum (Figs 10D, 11D). Scutellum not margined, sometimes a weak, non-projected posterior margin visible (Figs 8C, 8D, 10C, 11C). Notauli more widely separated and usually broader (Figs 8D, 8E). Scutellar foveae oval or rounded, deeper. Supapical setae of ventral spine of hypopygium short, not projected beyond the apex of the spine (Figs 15C, 15E). Frontal carina usually present; front and vertex punctate, usually with a coriarious-rugose sculpture (Figs 1C, 1D, 2B). Metasomal tergum T2+3 with or without micropunctures posteriorly **4**

3 Head from the dorsal view less than 2.5 as wide as long (Fig. 3B). POL 1.5 to 1.8 as long as OOL; OOL less than two times the diameter of a lateral ocellus. F1 slighter longer than F2 (Fig. 5J). Scutellum coriarious ..... ***Synergus elegans* sp. n.**

● Head strongly transverse in dorsal view, more than 2.5 times as wide as long (Fig.

3C). POL about 1.2 as long as OOL; OOL more than two times the diameter of a lateral ocellus. F1 as long as F2 (Fig. 5B). Scutellum with some transverse rugae **.....**

.....*Synergus laticephalus* sp. n.

4. F1 1.5 times as long as F2 (Figs 5C, 5H). F1 in males strongly expanded apically (Figs 6G, 6H). Frontal carinae indistinct, obscured by very irregular and branched interrupted rugae (Figs 1C, 1D). Facial striae irregularly sinuate, branched near the ventral margin of the eyes. Basal cell of forewing densely setose; veins darkly pigmented (Figs 17C, 17D). Metasomal T2+3 not punctate posteriorly. Body coloration predominantly reddish to black (Figs 18D, 18F)**..... 5**

● F1 as long as F2, or at most 1.2 longer than F2 (Figs 5D, 5E, 5L). F1 of males usually only slightly expanded apically, or slightly expanded basally and apically (Figs 6D, 6E, 6J). Frontal carinae usually distinct, sometimes branched before reaching the lateral ocelli (Figs 2A-F). Facial striae regular, sharp, not branched near the ventral margin of the eyes. Basal cell of forewing much less densely setose; veins usually paler (Figs 17G-J). Metasomal T2+3 punctate or not. Body coloration predominantly yellowish to yellow red (Figs 19A, 20F)**..... 6**

5 POL shorter than OOL (Fig. 3E). Frons with strong irregular rugae, with the intervals punctate (Fig. 1D). Sculpture of mesopleuron strong; the longitudinal carina dense and extended over the speculum (Fig. 10D). Radial cell less than 2.4 as long as wide (Fig. 17D). Face yellow, metasoma red, legs black (Fig. 18D) **.....**

..... *Synergus mesoamericanus* Ritchie & Shorthouse

● POL longer than OOL (Fig. 3F). Frons without irregular rugae and more closely punctuate (Fig. 1C). Sculpture of mesopleuron weak; with only a few longitudinal carinae medially with coriarious sculpture in the intervals and speculum partially smooth (fog. 10C). Radial cell 2.8 as long as wide (Fig. 17C). Predominantly black coloration (Fig. 18F) **.....*Synergus ramoni* sp. n.**

6 Forewing with a shaded infuscate area over the radial cell and extended beyond the Rs vein (Fig. 17E); radial cell short and wide, less than 2.5 as long as wide. F1 three times as long as pedicel (Fig. 5E). Metasomal T2+3 punctate posteriorly with the punctures extended over about 1/3 of the total length of the segment (Fig. 13E) **.....**

..... *Synergus nicaraguensis* Díaz & Gallardo.

● Forewing hyaline, without shaded infuscate areas; radial cell relatively longer, 2.6 to 3 times as long as wide (Figs 17G-J). F1 usually less than 2.6 times as long as the

pedicel (Figs 5F, 5G, 5L), if close to three times as long, then forewing hyaline. Metasomal T2+3 posteriorly punctate or not, if present, punctures usually extended over a narrower area **7**

7 Scutellar foveae large, quadrangular or irregularly rounded (Fig. 8D). Notauli deep, broad, broadening and converging posteriorly. Scutellum subpentagonal, strongly reticulate-rugose dorsally. Frons and vertex with a reticulate-rugose sculpture (Figs. 2D, 4G). Mesopleuron with a mixed striate-rugose sculpture, the intervals with coriarious sculpture (Fig. 11D). Facial carina sharp, widely spaced (Fig. 2D). Metasoma black dorsally with the notauli posteriorly reddish. Metasomal T2+3 with punctures extended about 1/3 of the metasomal length (Fig. 13C)

..... ***Synergus rufinotaulis*** **sp. n.**

● Scutellar foveae usually smaller, oval or ellipsoidal (Figs. 9A-D). Notauli not as deep, narrower and less convergent posteriorly. Scutellum rounded with a weaker rugose sculpture. Frons and vertex less strongly sculptured, punctate or rugose punctuate (Figs 2A-C). Mesopleuron usually with a striated, regular sculpture (Figs. 11A-C). Facial carina more closely spaced. Metasomal T2+3 with punctures usually forming a band, extended about 1/4 of metasomal length. Mesosoma dorsally with a different coloration. **8**

8 Metasomal T2+3 conspicuously punctate posteriorly, with the fine punctures extending about one third of the total length of the tergum (Fig. 14D). Mesoscutum with strong, closely spaced, interrupted, sinuate, transverse rugae (Fig. 9B). Frontal carinae narrow, branched close the lateral ocelli (Fig. 2F). Reared from stem, integral, no detachable galls **9**

● Metasomal T2+3 with punctures less visible, with the punctures forming a narrow band or only a dorsal patch (Figs. 14A, 14C). Mesoscutum coriarious with weak interrupted transverse rugae (Fig. 9A), or with stronger rugae, but then more widely spaced (Fig. 9D). Frontal carinae either narrow, branched, or wide and not branched (Fig. 2C). Reared from integral or detachable galls

..... **10**

9 F1 of female antenna as long as F2 (Fig. 5D); F2 of male strongly expanded apically (Fig. 6I). Ventral margin of clypeus not projected over mandibles. Genae not expanded behind eyes. Radial cell 2.8 as long as wide; venation darkly pigmented. Body reddish and black; basal half of metacoxae black in both sexes (Figs. 19C, 19D) .....

.....*Synergus colombianus* Nieves-Aldrey

● F1 1.2 as long as F2 (Fig. 5G); F2 of male slightly expanded apically (Fig. 6E). Ventral margin of clypeus slightly projected over mandibles. Genae expanded behind eyes. Radial cell long and narrow, slightly more than three times as long as wide, venation pale. Body yellowish with basal half of metacoxae entirely yellow in both sexes (Figs. 20F, 20G) **.....*Synergus luteus* sp. n.**

10. Frontal carina broad, not branched, or only branched close to the lateral ocelli. F1 1.1 to 1.2 as long as F2. Mesoscutum either with strong, widely spaced transverse rugae, or with a weak coriarious sculpture with very weak transverse rugae. **..... 11**

● Frontal carina narrow and branched (Fig. 2A, 4D). F1 1.3 as long as F2 (Fig. 5L). Mesoscutum weakly coriarious with some minute, closely spaced transverse rugae (Fig. 9A) .....

. **..... *Synergus gabrieli* sp. n.**

11 Sculpture of mesoscutum weakly coriarious with some weak transverse rugae (Fig. 9C). F1 of female antenna 2.8 as long as pedicel; 1.2 as long as F2 (Fig. 5F). Lateral propodeal carinae moderately convergent. Radial cell three times as long as wide, venation well pigmented (Fig. 17J) **.....*Synergus baruensis* sp. n.**

● Mesoscutum sculpture with strong, widely spaced, interrupted transverse rugae (Fig. 9D). F1 of female antenna 1.9 as long as pedicel; 1.1 as long as F2 (Fig. 5I). Lateral propodeal carinae strongly convergent (Fig. 12A). Radial cell less than three times as long as wide, venation pale (Fig. 17H)**..... *Synergus chiricanus* sp. n.**

Phylogenetic analysis

Results

A heuristic search with PAUP (majority rule analysis) found two shortest trees. The bootstrap analysis of the consensus tree is shown in Fig. 23B The analysis recovered three well-supported monophyletic groups, one close to *Saphonecrus lusitanicus*, another composed of *Agastoroxenia* as sister group of the core Panamanian *Synergus* species, including the Palaearctic species *S. ibericus* and a third monophyletic clade composed of *S. mesoamericanus* and the new species *S. ramoni*.

Discussion

The expected and observed diversity of inquilines of oak gall wasps from Panama.

It is generally assumed that there is a positive correlation between the number of *Quercus* species and their associated host gall-inducing and inquiline fauna. The richness of the Panamanian flora, with 9 *Quercus* species present, led us to believe that a richer, previously unsampled, fauna of inquilines of oak gall wasps awaited discovery in this country. This hypothesis has been confirmed by the results of this study. In comparative terms, the total of nine species of *Quercus* in Panama is close to the number of 10 species present in the Iberian peninsula (Nieves-Aldrey 2001). The number of inquilines of oak gall species found in Panama is eleven, which are from two genera, while thirty species from four genera have been recorded from Iberia, which is a geographic area that is much larger in size. Furthermore, it must be emphasized that the sampling effort has been considerably smaller in the case of the single study made in Panama, and more inquiline species will surely be found and added to the list of cynipid inquilines in Panama after further sampling. In this respect, our results indicated that more undescribed species could be present in our studied materials, although they have not been formally described here because of the low number of individuals available or due to their poor condition or their poor associated biological data. Therefore, even more cryptic *Synergus* diversity might be uncovered if sequence data of the studied samples were examined. According to our results, the richness of the Neotropical fauna is clearly much greater than expected, being close to the richness observed in the Oriental region (Abe *et al.* 2007) and much closer to the cynipid richness of the western Palaearctic and Nearctic faunas than was previously assumed (Nieves-Aldrey 2001; Ritchie & Shorthouse 1987; Csoka *et al.* 2005; Melika *et al.* 2005).

Relationships of the Holarctic and the Neotropical Synergus species

We found a clear taxonomic separation between the Palaearctic species and the Neotropical species, specifically the absence in all of the Neotropical species studied of a lateral pronotal carina. The presence of a lateral pronotal carina appears to be a derived character state in the Palaearctic *Synergus*. While the lateral pronotal carina is absent in all of the studied Neotropical species, most Palaearctic species have a distinct pronotal carina, but it is indistinct or absent in *Synergus plagiotrochi* Nieves-Aldrey &

Pujade-Villar, *S. variabilis* Mayr and *S. flavipes* Hartig, which are basal species close to the genera *Saphonecrus* and *Synophrus,* and all of these species are associated with cynipids on *Quercus* from the section *Ilex* or *Cerris*. Whether or not this implies the taxonomic separation of the genus into two different genera will be a matter of discussion in further studies after sequence data are analyzed.

Biology. Quercus section associations

Our analysis of the host plant associations of the west Palaeartic fauna of inquilines shows a strong specificity within different sections of *Quercus*, subgenus *Quercus*. The species associated with *Quercus* of the sections *Cerris* and *Ilex* are quite distinctive and more basal than the species linked to *Quercus* species of the section *Quercus*. One remarkable observation is that no inquilines species share *Quercus* hosts belonging different *Quercus* sections. For the studied Panamanian species, the specificity with respect to the different *Quercus* sections can be traced in our data matrix (character 63, Appendix 1). It is striking that the specificity for host plant is not as strong as for the Palaearctic species, and at least one species, *S. elegans*, is associated with *Quercus* hosts belonging to two sections: *Quercus* and *Lobata*, while six species are associated only with galls on plants of the *Quercus* section: *S. mesoamericanus, S. nicaraguensis, S. luteus, S. gabrieli, S. chiricanus* and *S. rufinotaulis*; and four species, *S. laticephalus, S. ramoni, S. baruensis* and *S. colombianus*, are linked to *Quercus* of the *Lobata* section. Tracing this biological character on the tree presented in Figure 23B indicates that, in comparison to the Palaearctic species, the phylogenetic signal of this character is weaker, or less indicative of a phylogenetic relationship in these Neotropical species.

Reliability and use of morphological characters in the taxonomy of Synergus

A number of weaknesses and flaws have been found in the current taxonomy and classification of *Synergus* based on morphological characters, as the failure of barcodes to discriminate among recognized morphological species has recently been shown, and the existence of cryptic lineages within several morphologically determined *Synergus* species was not recognized by morphological taxonomy. We believe that such mistakes have been caused in part by the limited set of morphological characters traditionally used in the taxonomy of this group or by errors in the identification of these species by

different taxonomists. In this study, we found that some characters that have been neglected or ignored in classical studies are useful in the diagnosis and identification of *Synergus* species. Among these useful characters are the following: the shape and distinctness of the facial striae; the relative size and shape of the basal tooth of metatarsal claw; the shape of the lateral carinae of the propodeum; the shape of the anterolateral pubescence on TA3; the shape and pilosity of the hipopygium and the pubescence on the basal cell of forewing. It is also important acquire good SEM images of the surface sculpturing of the frons, vertex, mesoscutum and mesopleuron because some interpretations based on artists' line drawings are weakly reliable and difficult to use for comparisons and descriptions.

Mayr´s sections

Mayr (1872) divided the genus *Synergus* into two sections based in part on their morphology (presence/absence of micropunctures on the posterior area of the large fused metasomal tergite) and biology (univoltine, or bivoltine without morphological differences between generations, versus bivoltine, usually with a strong difference between generations). This long-accepted division has recently been challenged as unnatural based on barcoding data (Ács *et al.* 2010). Our results from a set of Neotropical species are ambiguous with respect to this debate. The tracing of a morphological character state (51, Appendix 1) in our morphological phylogenetic tree (Fig. 23B) is congruent with the monophyletic groups recovered in this study and, thus, indicates that the character of the metasomal sculpture is not as highly homoplaxic or evolutionarily labile as supposed (Ács *et al*. 2010). However, there seems no correlation between this character state and the life cycle in the case of the studied Neotropical species, as was observed by Mayr (1872) for the European species.

Future work

This study found evidence that the rich fauna of previously undescribed inquiline species of oak gall wasps found in this study in Panama might represent only a fraction of the actual diversity that exists. Much more sampling will be required to achieve a deeper understanding of this fauna, especially with regard to the previously unsampled community of subterranean oak gall species and the cryptic galls in twigs, which usually host specific inquiline faunas. Until now, very little was known about the life

cycles, immature stages, food webs, parasitoids, community structure and other aspects of the biology and ecology of the Panamanian species here studied, and much more field work will be needed in the future to fill these scientific gaps. Obtaining sequence data for the studied species and performing molecular phylogenetic studies of this fauna is also an obvious priority for future research in this group of species. Hopefully, these type of studies are s taking place as part of ongoing international projects.

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Appendix 1. List of characters and character states used for phylogenetic analysis

Explanation of abbreviations used in the character descriptions (*x* refers to an integer): A*x* = antennomere *x*; F*x* = flagellomere *x*; *x*T = abdominal tergum *x*.

Head, anterior view, female

1. Ratio of width /height of the head (0) oval o rounded; as wide as high (ratio 1-1.1) (1) slightly trapezoid, slightly wider than high (ratio 1.22-1.25) (2) transverse; clearly wider than high (ratio 1.34-1.41).
2. Shape of genae, (0) not expanded behind compound eyes (Figs. 1E, 3B) (1)

slightly expanded behind compound eyes (2) strongly expanded (Figs. 1F, 3D)

3. Shape of ventral margin of clypeus: (0) straight or slightly sinuate, not projecting over mandibles (Fig. 2E) (1) slightly projecting over mandibles (Fig. 1B).
4. Facial striae radiating from lateral clypeus: (0) long, reaching eye margins, toruli and laterally extending into genal area (1) short, not reaching toruli and not extending over genal area.
5. Distinctness of facial striae (0) iregular, low, weak, not widely spaced (Fig. 1A) (1) regular, higher, stronger, more widely spaced (Fig. 2D). (2) strong and deep but closely spaced.
6. Shape of apical end of facial striae (0) regular, not branched close compound eyes (Fig. 2D) (1) irregular, sinuate or undulate, branching close margin compound eyes (Fig. 1C).
7. Frontal carinae: (0) absent (Fig. 3A) (1) present (Fig. 3D).
8. Distinctness and shape of frontal carinae (0) narrow and incomplete, faint or branched before reaching lateral ocelli (Fig. 3E) (1) narrow, somewhat branched but reaching lateral ocelli (2) complete, wide and not branched (Fig. 2C).
9. Distance between toruli, compared to diameter of a torulus, including rim: (0) short, subequal or shorter than half diameter (0,35-0,5) (Fig. 1C) (1) long; more than 0,6 diameter of a torulus (Fig. 1A).
10. Distance between mesal margin of compound eye and lateral margin of a torulus: (0) shorter than diameter of a torulus included rim (0,5-0,85) (Fig. 2D) (1) as long as or a little longer than diameter of a torulus (Fig. 1A).
11. Relative position of toruli on face; distance of ventral margin of toruli to ventral margin of compound eye: (0) high, distance 1.6-2 times diameter of a torulus; (1) intermediate, 1- 1,5 times diameter (2) low, subequal to shorter than diameter.
12. Length of malar space: (0); short 0,3-0,6 veces as long as length of compound eye (1) long, 0,8 as long as compound eye (Fig. 1B).
13. Sculpture on frons: (0) weakly coriarious (1) coriarious rugose, with some rugae dorsally.

14. Punctures on frons: (0) absent (Fig. 1A) (1) present (Fig. 3F).

Head dorsal view

15. Sculpture on vertex: (0) weakly coriarius (1) slightly rugose (2) strongly rugose
16. Punctures on vertex: (0) absent (1) present, weak (2) present, strong.
17. Ocellar triangle (POL/OOL): (0) POL shorter tan OOL (Fig. 3E) (1) 1.4 a 1.8 longer tan OOL (Fig. 3F) (2) more than 2 times OOL (2-2.4).
18. Size of ocelli (OOL/diameter of lateral ocelli: (0) OOL shorter than diameter (Fig. 3F) (1) 1-1.4 times as long as diameter (2) 1.7 - 1.9 veces (3) more than 2 times (2.2) (Fig. 3C).

Head posterior view

19. Sculpture on dorsal region of occiput (0) coriarious (1) rugose.
20. Punctures on dorsal region of occiput (0) absent (1) present.

Antennae, female

21. Number of completely separated flagellomeres: (0) 11 (1) 12 (2) 13
22. Length scape (0) 1-1,5 times as long as pedicel (1) 1,6-1,8 (2) 2 times as long as pedicel.
23. Ratio length/width of pedicel (0) short, 1-1,5 as long as wide (Fig. 5C) (1) 1.6-1.8 times as long as wide (2) more than 2 times as long as wide (2.2-2.6) (Fig. 5A).
24. Ratio A3/A2 (0) 1.5-1.7 (1) 1.9-2.3 (2) 2.5-2.7 (3) 2.9-3.
25. Length of F1 (0) short, about as long as F2 (Fig. 5D) (1) 1.2-1.3 as long as F2 (2) about one and a half as long as F2 (1.42-1.47) (3) about two times as long as F2 (Fig. 5A).

Antennae, male

26. Shape of F1 (0) weakly curvate and excavate medially, slightly expanded basally and apically (1) weakly curvate and excavate medially, slightly expanded apically (Fig. 6B) (2) weakly curvate and excavate medially, strongly expanded apically (Fig. 6I) (3) strongly curvate and excavate

medially, the ventral margin strongly convex, strongly expanded basally and apically (Fig. 6A).

27. Number of completely separated flagellomeres (0) 13 (1) 12 (2) 11

Pronotum, female

28. Lateral pronotal carina (0) absent (Fig. 7B) (1) present (Fig. 7A).
29. Sculpture on lateral pronotal surface (0) coriarious (1) coriarious-rugose, the rugae more or less conspicuous.
30. Shape of pronotum, lateral view (0) short, about as long as high (1) long, much more longer than high

Mesoscutum

31. Sculpture of mesoscutum (0) coriarious (Fig. 8A) (1) coriarious-rugose, with transverse rugae more or less marked (Fig. 8C).
32. Shape of the transversal rugae of mesoscutum (0) closely spaced (1) widely spaced, the interspaces more broad.
33. Shape of the notauli (0) percurrent and distinct (Fig. 8C) (1) almost percurrent, but anterior half indistinct or faint (Fig. 8A)
34. Median mesoscutal impression (0) entirely absent or invisible (1) present, indicated at least as a slight impression at posterior margin of mesoscutum (Fig. 8F).
35. Extension of median mesoscutal impression (0) short and superficial, indicated only as a slight impression at posterior margin of mesoscutum (1) longer and more deeply impressed, reaching or surpassing mid region of mesoscutum.
36. Width of notauli (0) shallowly impressed and narrow; posteriorly not wider than trasscutal fissure (Fig. 8B) (1) wider and deeply impressed, posteriorly wider than transscutal fissure (Fig. 8D).
37. Separation of notauli at the meeting with transscutal fissure (relative convergence of notauli posteriorly). (0) notauli weekly convergent posteriorly, widely separated at meeting with transscutal fissure; the distance between notauli margins 8.4 to 11.5 as breadth of a notaulus. (1) notauli more strongly convergent posteriorly, less widely separated at meeting with

transscutal fissure, the distance between notauli as 3.3 to 6.5 the breadth of a notaulus.

38. Shape of scutellar foveae (0) elipsoidal (Fig. 8E) (1) quadrangular (Fig. 8B) (2) rounded (Fig. 8D).
39. Anterior margin of the scutellar foveae (0) curved, widely divergent of the transscutal fissure, from the joining point of the foveae (1) more or less straight and then laterally divergent (2) straight along the entire anterior margin, and then forming an angle about 90º with the trasscutal fissure.
40. Posterior margin of the scutellar foveae (0) distinct (1) indistinct.
41. Distinctiness of the scutellar foveae (0) well impressed, deep and distinct (1) shallow, somewhat indistinct.
42. Dorsal surface of scutellum (0) not margined posteriorly and posterolaterally (Fig. 8E) (1) with a distinct flange, with distinct sharp margin posteriorly and posterolaterally (Fig. 8B).

Mesopleuron

43. Sculpture on speculum (0) horizontal carinae present (Fig. 10D) (1) smooth, not carinate (Fig. 10E).
44. Shape of the carinate sculpture of mesopleuron (0) regular, carinae sharp and narrow, the interspaces smooth (Fig. 11C) (1) irregular, carinae wider and blunt, the interspaces with coriarious sculpture (Fig. 11B) (2) mesopleuron with a mixed coriarious-reticulate and horizontally carinate sculpture (Fig. 11D) (3) horizontal carinae weak and reduced, the interspaces smooth (Fig. 10E).

Metapectal-propodeal complex

45. Lateral propodeal carinae (0) subparallel (Fig. 12C) (1) slightly convergent posteriorly anterior distance between carinae 1. 4 times as posterior distance between them (Fig. 12B) (2) strongly convergent posteriorly, anterior distance between carinae 1.7 times as posterior distance between them (Fig. 12A).

Legs

46. Basal tooth of the metatarsal claw (0) long, reaching more than 0.5 length of apical tooth (Fig. 16E) (1) short, not reaching half of length of apical tooth (Fig. 16B).

Metasoma, female

47. Anterolateral pubescence on TA3 (0) with a compact patch of setae ventro-laterad to abdominal petiole, extending towards dorsal region of tergite (1) group of the setae less compact, at least composed by 12 setae, and not extending towards dorsal region of tergite. (2) a group of few setae present extended also to dorsal region of tergite (3) only 2-3 setae visible (4) about 7 setae arranged on a vertical row.
48. Size of tergite TA3 (0) Almost covering entirely metasoma, remaining tergites almost invisible (Fig. 13A) (1) Not covering entirely metasoma, remaining tergites visible at least in part (Fig. 13D).
49. Shape of posterior margin of TA3 in lateral view (0) oblique, more or less straigth, forming a near 90° angle with dorsal margin of tergite (Fig. 13B) (1) rounded or curved, forming an obtuse angle with dorsal margin of tergite (Fig. 13E).
50. Ratio length/height of TA3 (0) short and high, about as long as high or slightly longer tan high (1) elongate, 1.2-1.4 times as long as high.
51. Micropunctures on posterior margin of TA3 + 4, (0) absent (1) present.
52. Extension of the micropunctures on posterior margin of TA3 + 4: (0) extended only on a small posterodorsal patch of tergite (1) forming a narrow band along the posterior margin (Fig. 14A) (2) Micropunctures extended at least to one-third of total length of tergite (Fig. 13E).
53. Length of projecting part of hypopigial spine (beyond attachment of lateral flap): (0) not projected behind attachment with sternite (Fig. 15B) (1) slightly projected (2) clearly projected (Fig. 15F).
54. Lateral pubescence of hypopigial spine (0) sparse, spaced, rows with 6-7 setae only (1) pubescence more dense and closely spaced, rows with 10 or more setae.
55. Apical setae of hypopigial spine (0) short, not projecting or only slightly projecting beyond apex of spine (Fig. 15E) (1) long, far projecting apex

spine (Fig. 15A).

Forewing, female

56. Anterior margin of radial cell: (0) open; R1 ending at wing margin (1) ambiguous state, R1 depigmented, paler along wing margin, the radial cell appearing virtually open (Fig. 17B) (2) unambiguous closed, the R1 vein well pigmented, continuing along wing margin until reaching Rs. (Fig. 17C).
57. Wing coloration: (0) hyaline, without smoky or infuscate areas (1) with a heavily infuscate area on the radial cell.
58. Length of radial cell: (0) short and wide ; less than 2.5 times as long as wide (2.2-2.3) (1) intermediate length, 2.5-2.8 times as long as wide (2) long, about 3 times as long as wide.
59. Areolet: (0) inconspicuous (Fig. 17E) (1) conspicuous, clearly visible (Fig. 17D).
60. Definition of Rs+M: (0) invisible (1) visible at least in part (2) clearly visible-
61. Pubescence of basal cell (0) dense, closely spaced setae covering the basal cell (Fig. 17C) (1) scarce, few setae and more widely spaced (Fig. 17J).
62. Length of fringe of setae on apical margin: (0) short (Fig. 17D) (1) long (Fig. 17H).

Biology

63 Host plant section within *Quercus* subgenus attacked by the host gall wasp inductor: (0) *Quercus* (1) *Lobata* (2) *Quercus* and *Lobata* (3) *Ilex* and *Cerris*

64 Host plant gall attachment: (0) integral, fused with plant (1) detachable

65 inquiline specificity (0) monophagous (1) oligophagous (2) poliphagous

Table 1. Data matrix based on the characters listed in Appendix 1. "?" indicates missing data; "-" is used if the character is inapplicable.

Species	Characters 1	11	21	31
Synergus elegans	2 0 0 0 0 0 0 - 1 1	1 0 0 0 0 0 1 2 0 0	1 0 0 1 1 1 0 0 0 0	0 - 1 0 - 0 0 1 2 1
Synergus laticephalus	2 0 1 0 0 0 0 - 1 1	1 1 0 0 0 0 1 3 0 0	1 1 1 1 0 ? ? 0 0 0	0 - 0 0 - 0 0 1 2 1
Synergus mesoamericanus	0 0 0 0 1 1 1 0 0 1	2 0 1 1 2 2 0 2 1 1	1 1 0 2 2 2 0 0 1 0	1 0 0 1 0 1 1 0 0 0
Synergus ramoni	0 0 0 0 1 1 1 0 0 1	2 0 0 1 2 2 1 1 1 1	1 1 0 2 2 2 0 0 1 0	1 0 0 0 - 1 1 0 0 0
Synergus nicaraguensis	2 0 0 0 1 0 1 2 0 0	0 0 1 1 2 2 1 1 1 1	1 2 0 3 0 1 0 0 1 0	1 1 0 1 0 1 1 0 0 0
Synergus luteus	1 1 1 0 1 0 1 1 0 0	0 0 1 1 1 1 1 1 1 1	1 1 0 2 1 1 0 0 1 0	1 0 0 0 - 1 1 0 0 0
Synergus baruensis	1 1 0 0 1 0 1 2 0 0	1 0 1 1 1 1 1 1 1 1	1 1 0 3 1 1 0 0 1 0	0 - 0 0 - 1 1 0 1 0
Synergus gabrieli	1 0 1 0 1 0 1 1 0 0	1 0 0 1 1 1 1 1 1 1	1 0 1 2 1 1 0 0 1 0	1 1 0 0 - 1 1 0 1 0
Synergus chiricanus	1 1 0 0 1 0 1 2 0 0	1 0 1 1 1 2 1 1 1 1	1 1 0 1 0 1 0 0 1 0	1 1 0 0 - 1 1 0 0 0
Synergus rufinotaulis	1 0 1 0 1 0 1 1 0 0	0 0 1 1 2 1 1 1 1 1	1 2 0 3 0 1 0 0 1 0	1 1 0 1 0 1 1 2 1 0
Synergus colombianus	1 0 0 0 1 0 1 1 0 0	0 0 1 1 1 1 1 2 1 1	1 1 0 1 0 2 0 0 1 0	1 0 0 1 0 1 1 0 1 0
Synergus ibericus	1 0 0 0 1 0 1 2 0 0	0 0 1 1 2 2 2 0 1 1	1 1 0 3 0 1 0 1 1 0	1 0 0 1 1 1 1 0 2 0
Agastoroxenia panamensis	1 2 1 0 2 1 1 0 0 0	1 0 1 1 2 2 1 1 1 1	0 0 2 0 3 3 2 0 1 0	1 1 1 0 - 1 1 0 0 0
Saphonecrus lusitanicus	1 0 0 1 0 0 0 - 0 0	0 0 0 0 0 1 2 1 0 0	0 0 2 0 1 0 1 0 0 1	0 0 1 0 - 0 0 0 0 1

Species	Characters 41	51	61
Synergus elegans	1 1 1 3 0 1 2 0 0 1	0 - 1 1 1 1 0 1 0 0	0 0 2 1 2
Synergus laticephalus	1 1 1 3 0 1 3 0 0 1	0 - 0 1 1 1 0 1 0 0	0 0 1 1 0
Synergus mesoamericanus	0 0 0 1 1 ? 2 1 0 0	0 - 2 1 0 2 0 1 1 2	0 0 0 0 0
Synergus ramoni	0 0 1 2 0 1 2 0 0 1	0 - 1 1 0 2 0 2 1 2	0 0 1 1 0
Synergus nicaraguensis	0 0 0 1 0 0 3 1 1 0	1 2 0 1 0 2 1 0 0 2	1 0 0 1 0
Synergus luteus	0 0 0 0 1 0 1 0 1 0	1 2 0 1 0 1 0 2 0 1	1 1 0 0 1
Synergus baruensis	0 0 0 0 1 0 1 1 1 0	1 1 0 1 0 2 0 2 0 1	1 1 1 0 0
Synergus gabrieli	0 0 0 0 1 1 3 1 1 0	1 0 1 1 0 1 0 2 0 0	1 1 0 1 1
Synergus chiricanus	0 0 0 1 2 0 3 1 1 0	1 1 0 1 0 1 0 1 0 0	1 1 0 0 0
Synergus rufinotaulis	0 0 0 1 1 0 1 0 1 0	1 2 1 1 0 2 0 2 0 1	1 1 0 1 1
Synergus colombianus	0 0 0 0 1 0 1 1 1 0	1 2 1 1 0 2 0 1 0 1	1 0 1 1 0
Synergus ibericus	0 0 0 0 0 0 0 0 0 1	1 2 0 1 0 2 0 1 0 1	0 0 0 1 0
Agastoroxenia panamensis	0 0 0 1 0 1 4 0 0 0	0 - 1 0 0 0 0 1 0 1	1 0 0 0 0
Saphonecrus lusitanicus	1 0 0 0 0 ? 1 0 0 0	1 0 2 0 1 0 0 1 0 0	0 0 3 0 2

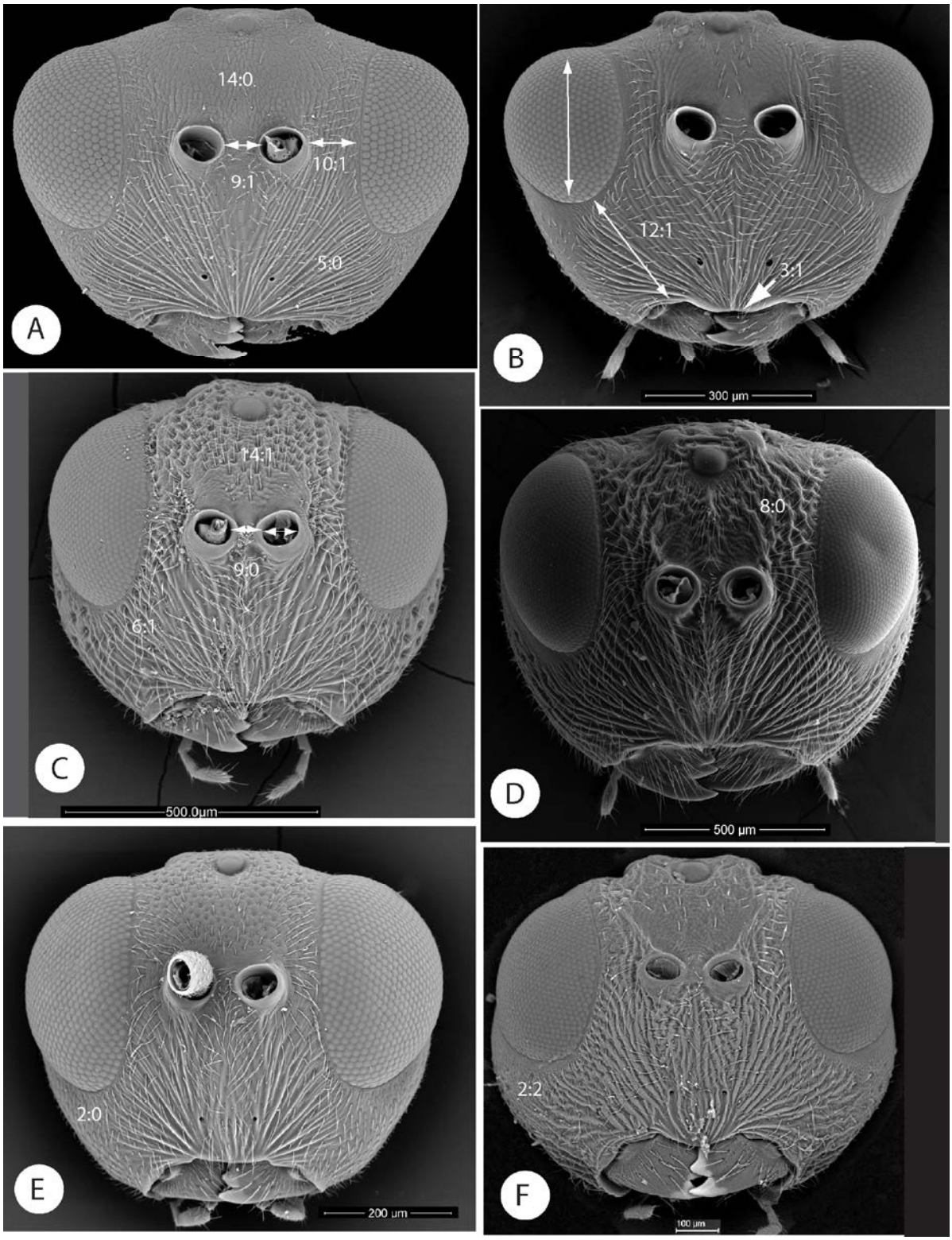

Figure 1. Head anterior view of inquilines of oak gall wasps: (A) *Synergus elegans*. (B) *Synergus laticephalus*. (C) *Synergus ramoni*. (D) *Synergus mesoamericanus*. (E) *Saphonecrus lusitanicus*. (F) *Agastoroxenia panamensis*.

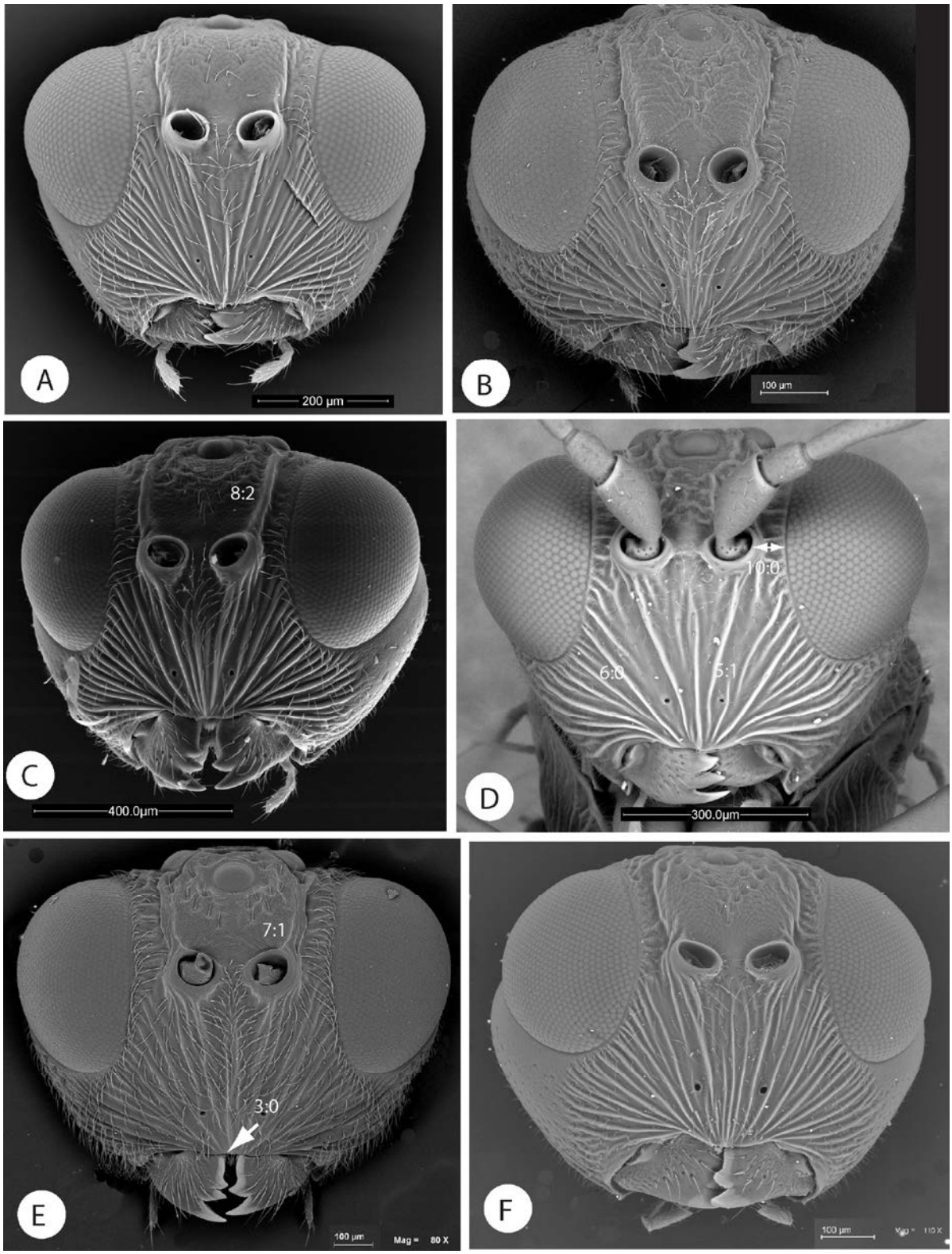

Figure 2. Head anterior view of *Synergus* species: (A) *Synergus gabrieli.* (B) *Synergus chiricanus.* (C) *Synergus baruensis.* (D) *Synergus rufinotaulis.* (E) *Synergus nicaraguensis*. (F) *Synergus luteus.*

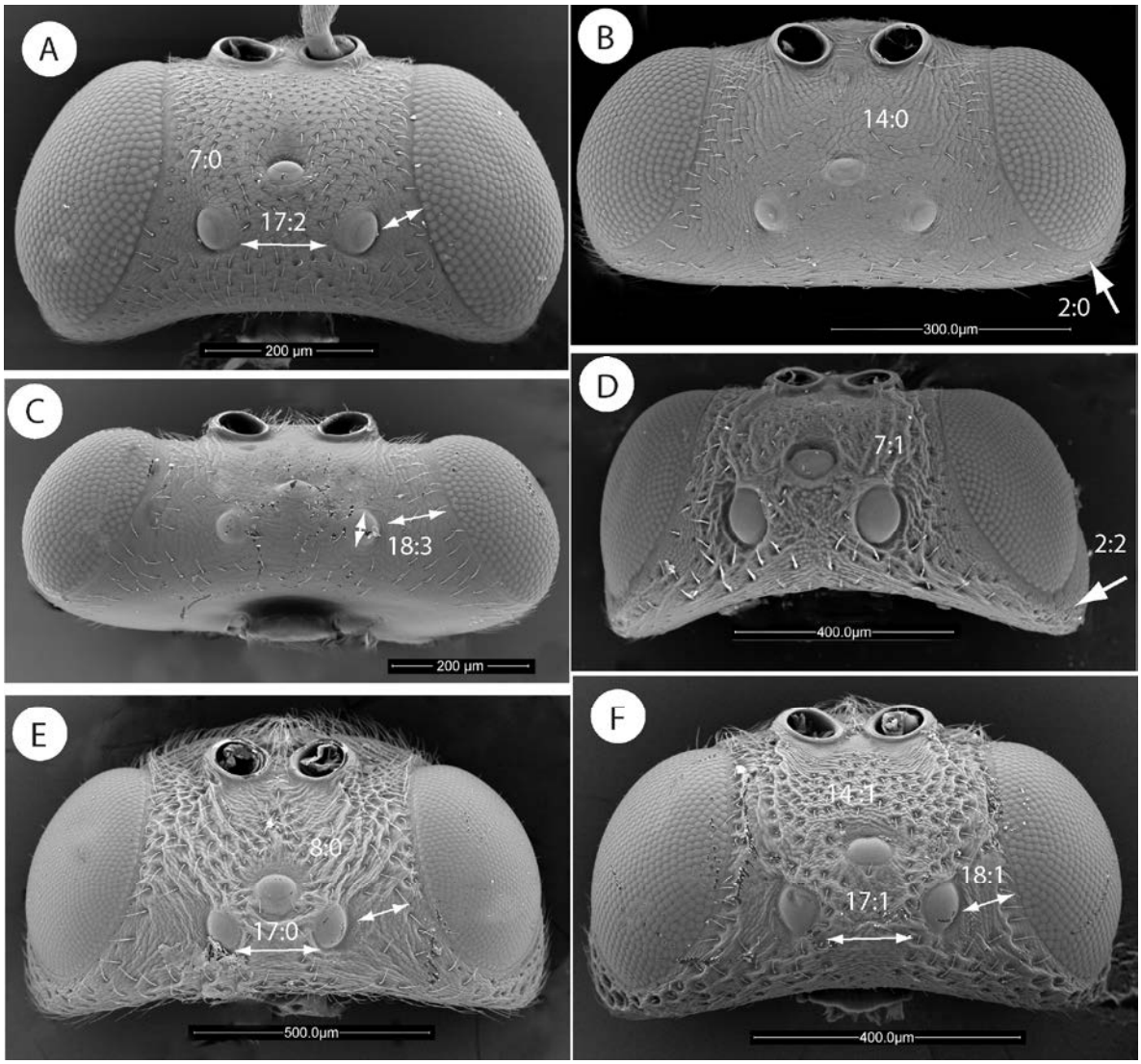

Figure 3. Head dorsal view of inquilines of oak gall wasps: (A) *Saphonecrus lusitanicus.* (B) *Synergus elegans.* (C) *Synergus laticephalus.* (D) *Agastoroxenia panamensis*. (E) *Synergus mesoamericanus.* (F) *Synergus ramoni.*

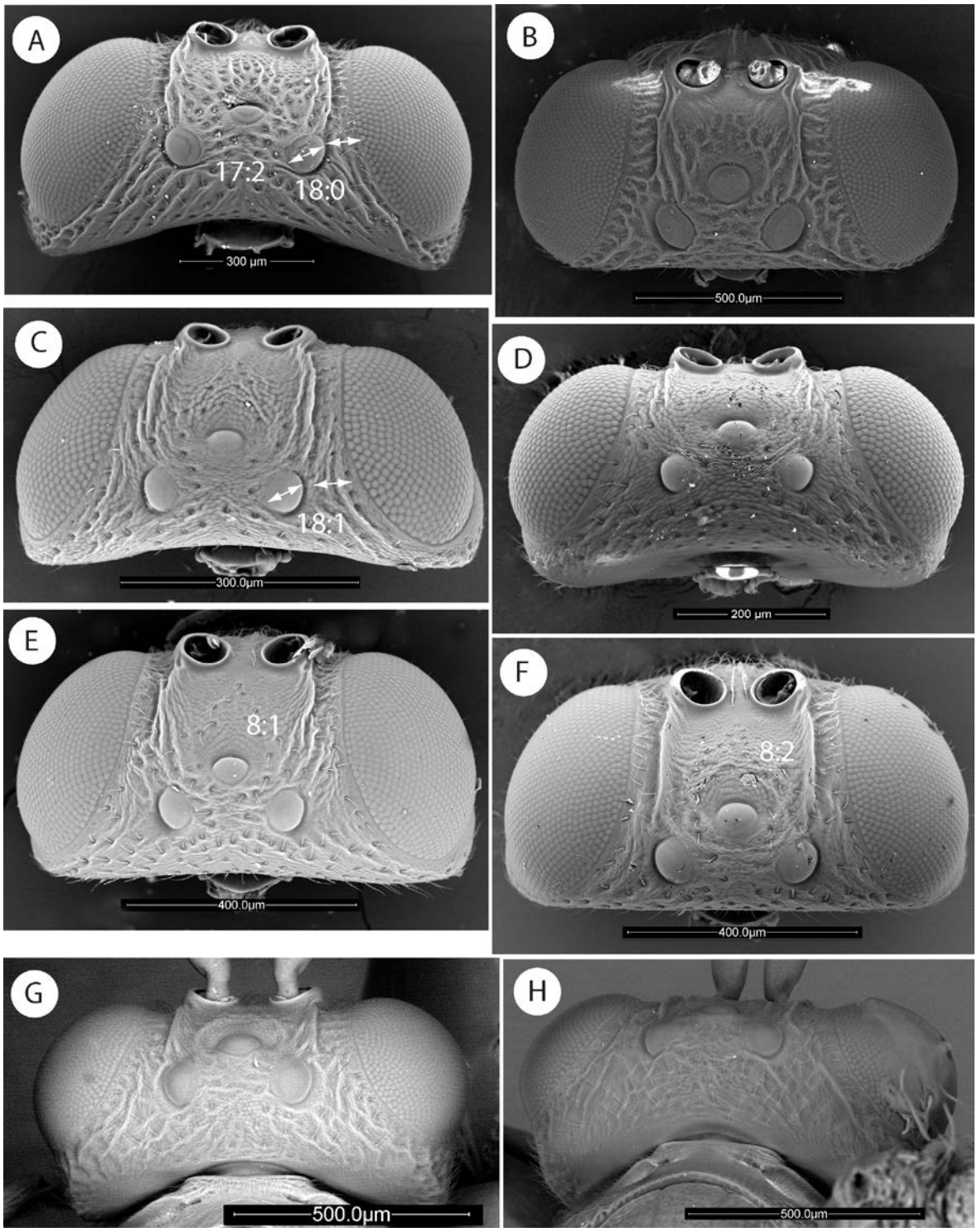

Figure 4. Head dorsal of *Synergus* species: (A) *Synergus ibericus*. (B) *Synergus nicaraguensis*. (C) *Synergus chiricanus*. (D) *Synergus gabrieli*. (E) *Synergus luteus*. (F) *Synergus baruensis*. (G) *Synergus rufinotaulis,* male. (H) *Synergus rufinotaulis,* female.

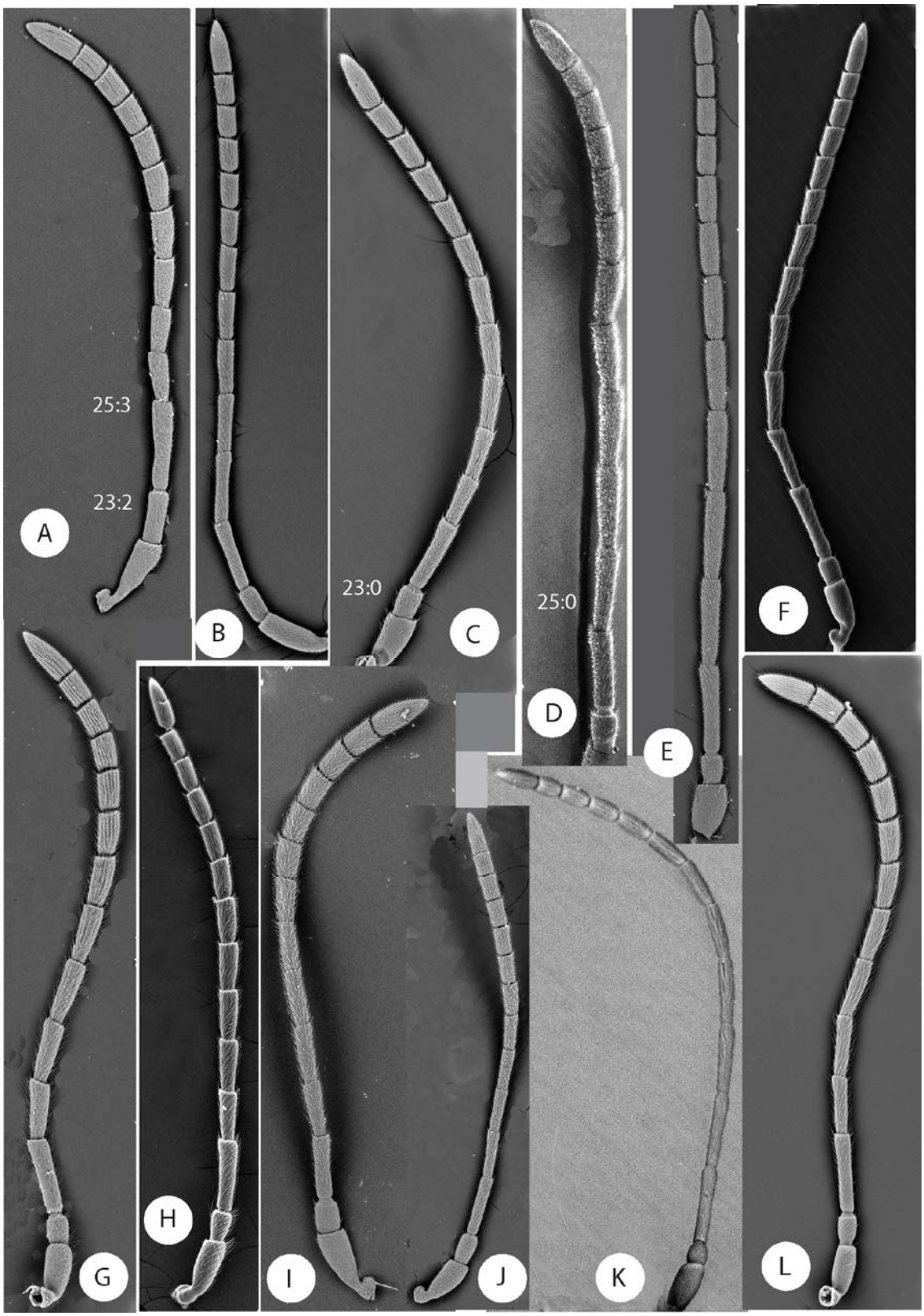

Figure 5. Female antennae of inquilines of oak gall wasps: (A) *Agastoroxenia panamensis*. (B) *Synergus laticephalus.* (C) *Synergus ramoni.* (D) *Synergus colombianus*. (E) *Synergus nicaraguensis*. (F) *Synergus baruensis*. (G) *Synergus luteus.* (H) *Synergus mesoamericanus.* (I) *Synergus chiricanus* (J) *Synergus elegans*. (K) *Synergus rufinotaulis*. (L) *Synergus gabrieli.*

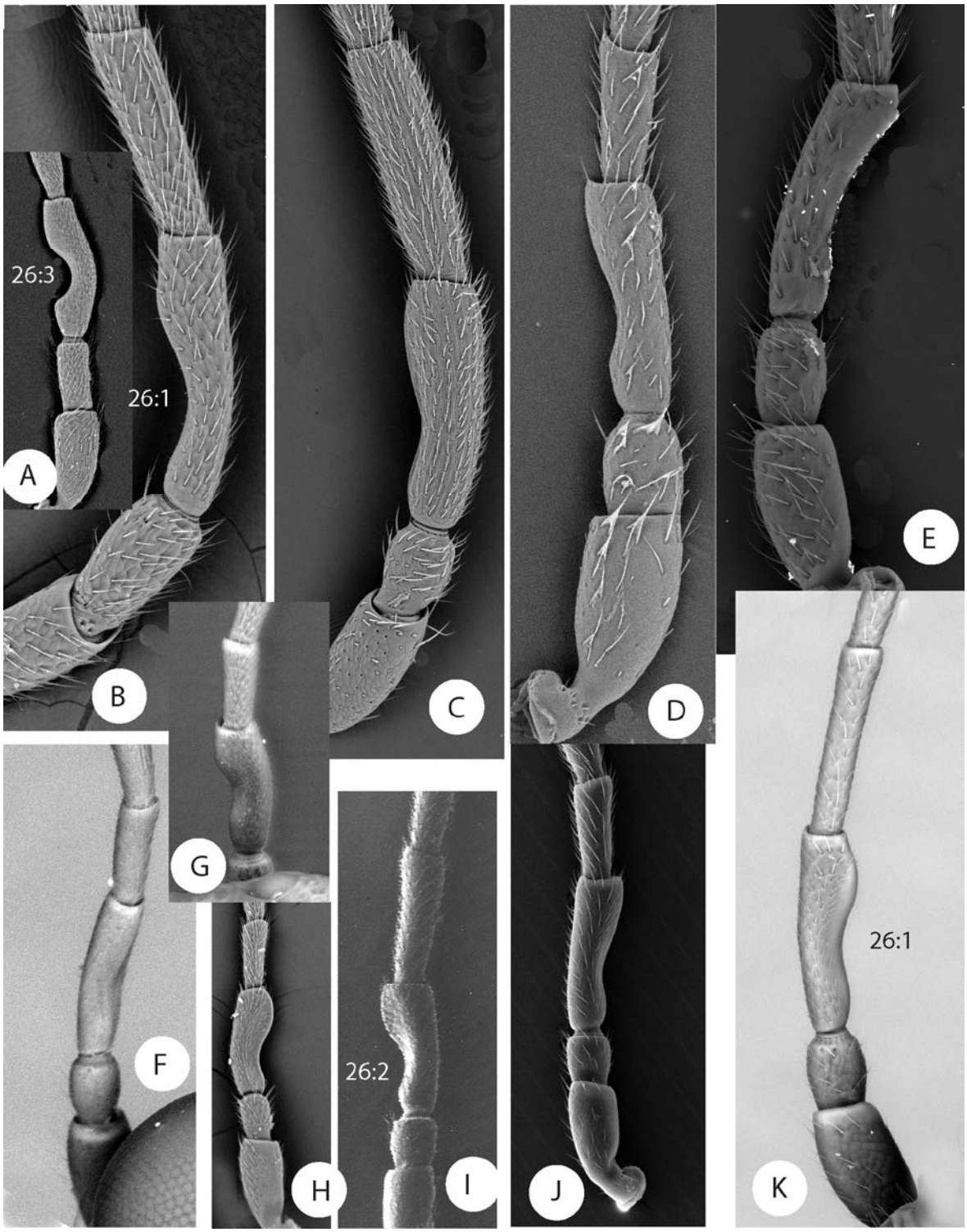

Figure 6. Male antennae of inquilines of oak gall wasps: (A) *Agastoroxenia panamensis*. (B) *Synergus elegans*. (C) *Synergus nicaraguensis*. (D) *Synergus chiricanus*. (E) *Synergus luteus*. (F) *Synergus gabrieli*. (G) *Synergus ramoni*. (H) *Synergus mesoamericanus*. (I) *Synergus colombianus*. (J) *Synergus baruensis*. (K) *Synergus rufinotaulis*.

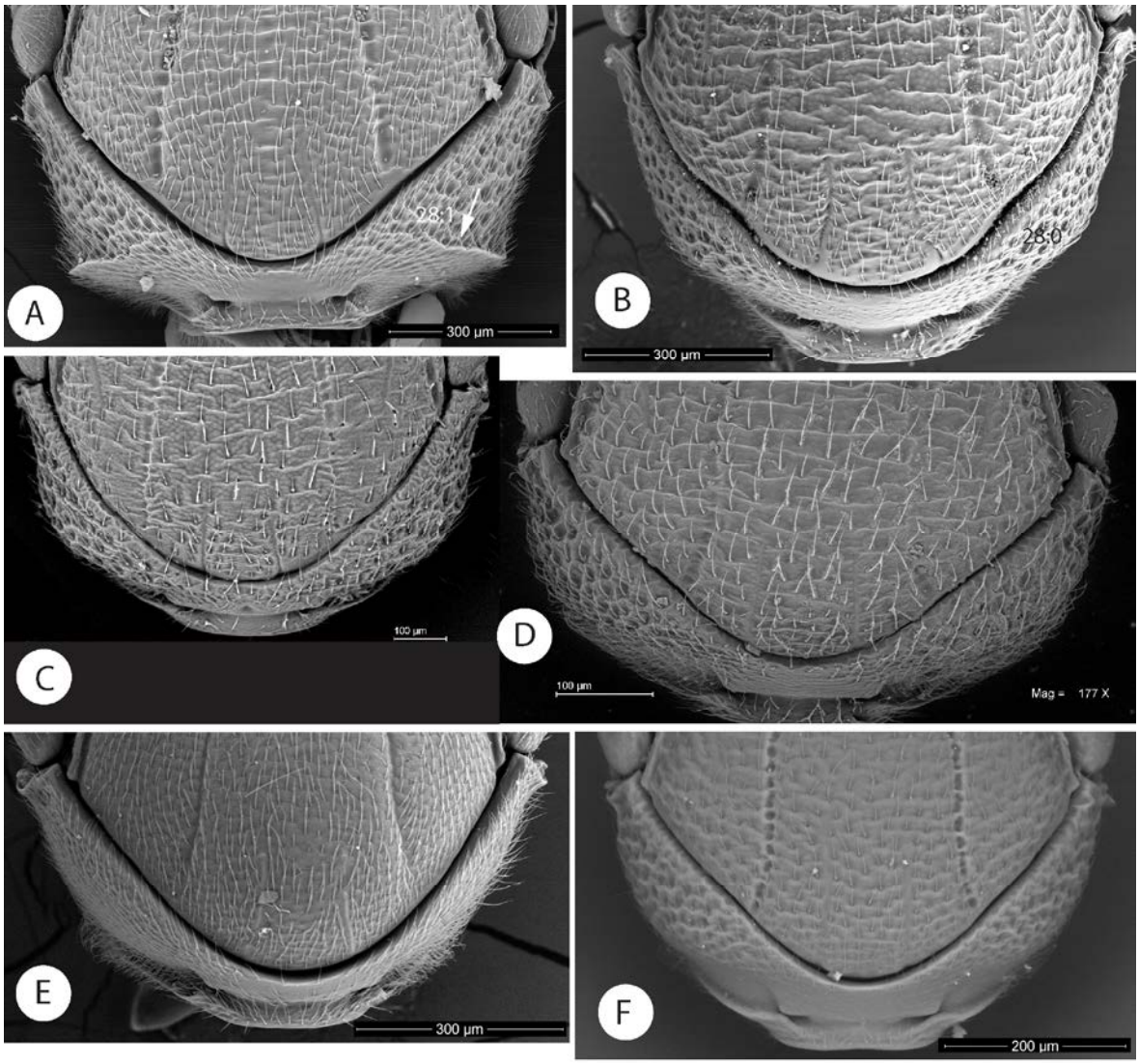

Figure 7. Pronotum anterior view of inquilines of oak gall wasps: (A) *Synergus ibericus*. (B) *Synergus ramoni.* (C) *Agastoroxenia panamensis*. (D) *Synergus chiricanus.* (E) *Synergus laticephalus.* (F) *Synergus gabrieli.*

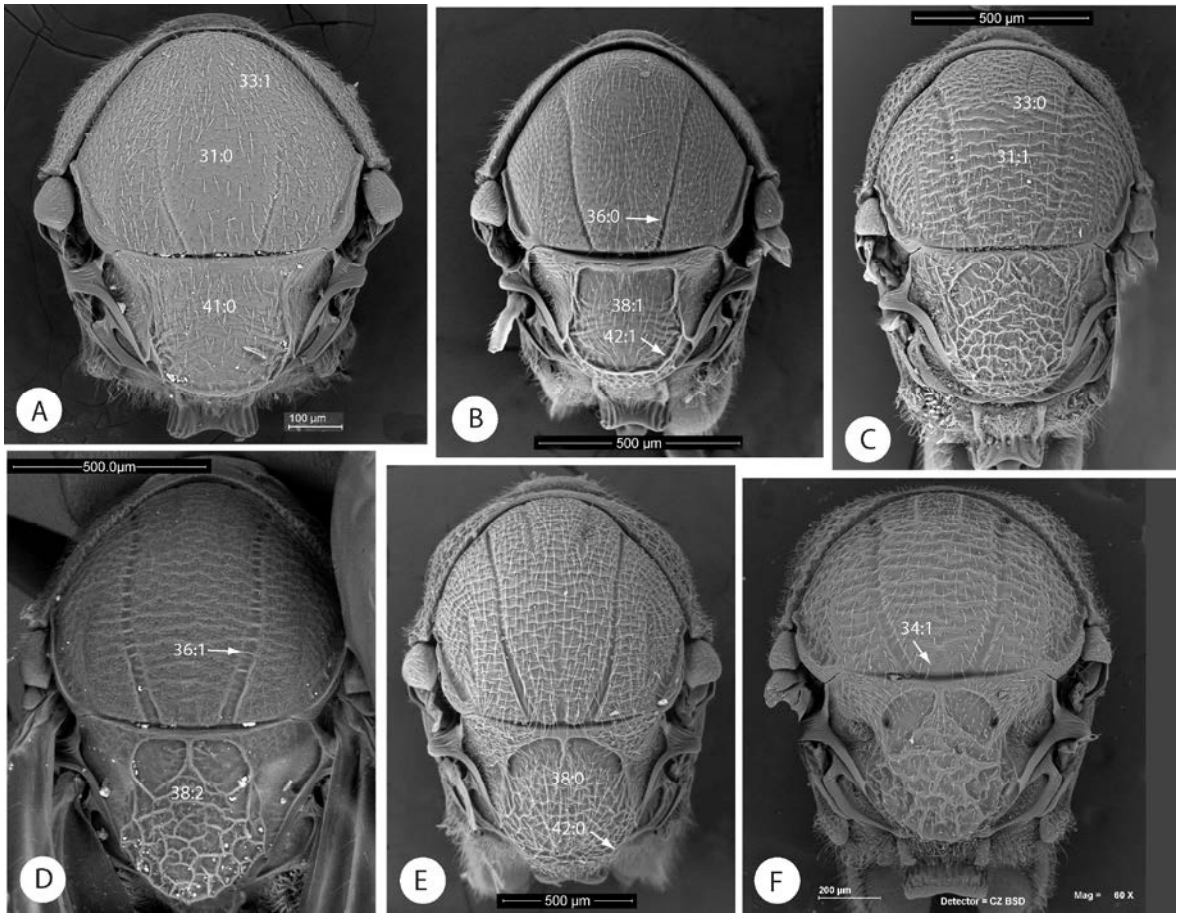

Figure 8. Mesosoma dorsal view of *Synergus* species: (A) *Synergus elegans*. (B) *Synergus laticephalus*. (C) *Synergus ramoni*. (D) *Synergus rufinotaulis*. (E) *Synergus mesoamericanus*. (F) *Synergus nicaraguensis*.

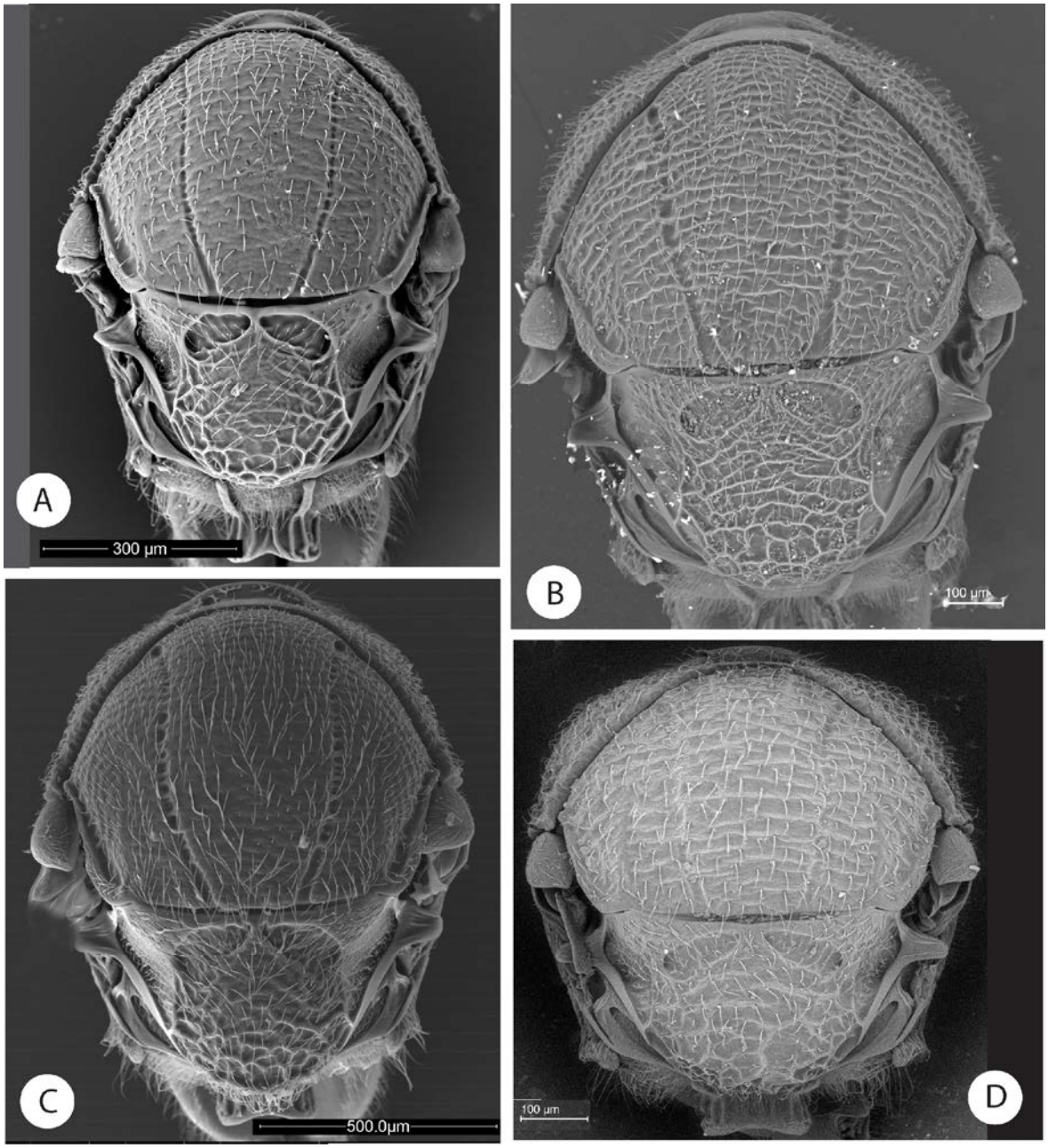

Figure 9. Mesosoma dorsal view of *Synergus* species: (A) *Synergus gabrieli*. (B) *Synergus luteus.* (C) *Synergus baruensis.* (D) *Synergus chiricanus.*

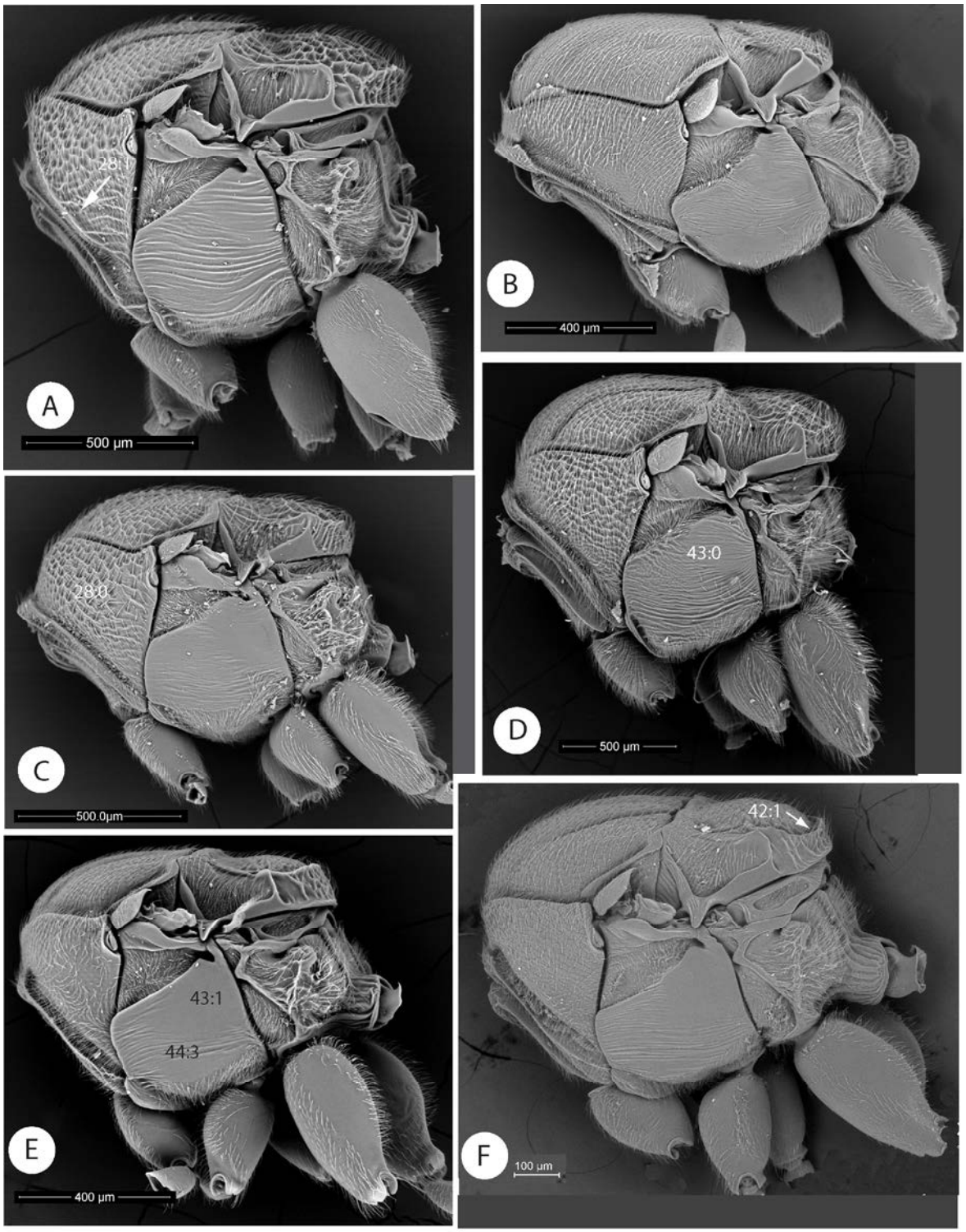

Figure 10. Mesosoma lateral view of inquilines of oak gall wasps: (A) *Synergus ibericus*. (B) *Saphonecrus lusitanicus.* (C) *Synergus ramoni.* (D) *Synergus mesoamericanus.* (E) *Synergus laticephalus.* (F) *Synergus elegans.*

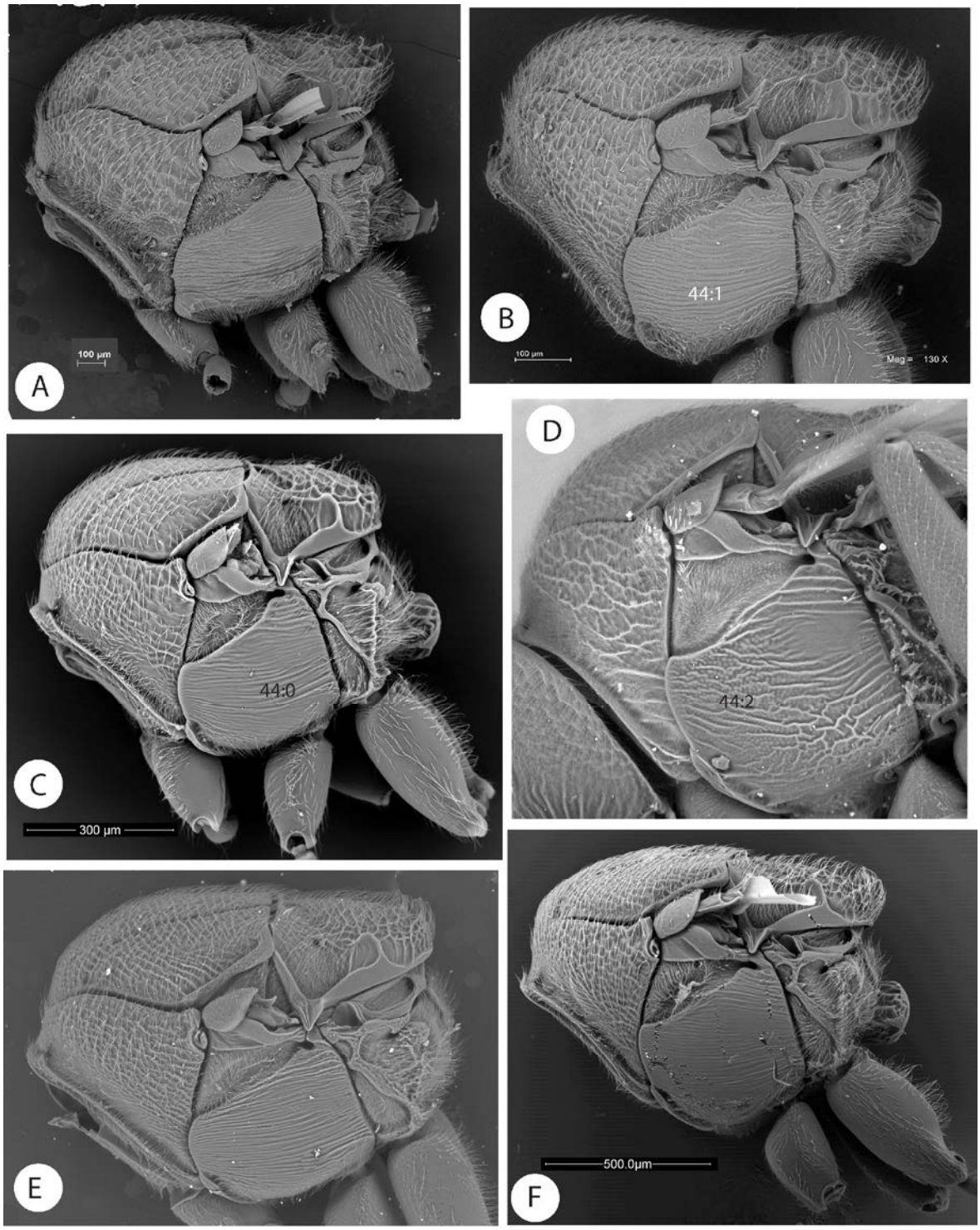

Figure 11. Mesosoma lateral view of inquilines of oak gall wasps: (A) *Synergus nicaraguensis*. (B) *Synergus chiricanus.* (C) *Synergus gabrieli.* (D) *Synergus rufinotaulis.* (E) *Synergus luteus.* (F) *Synergus baruensis.*

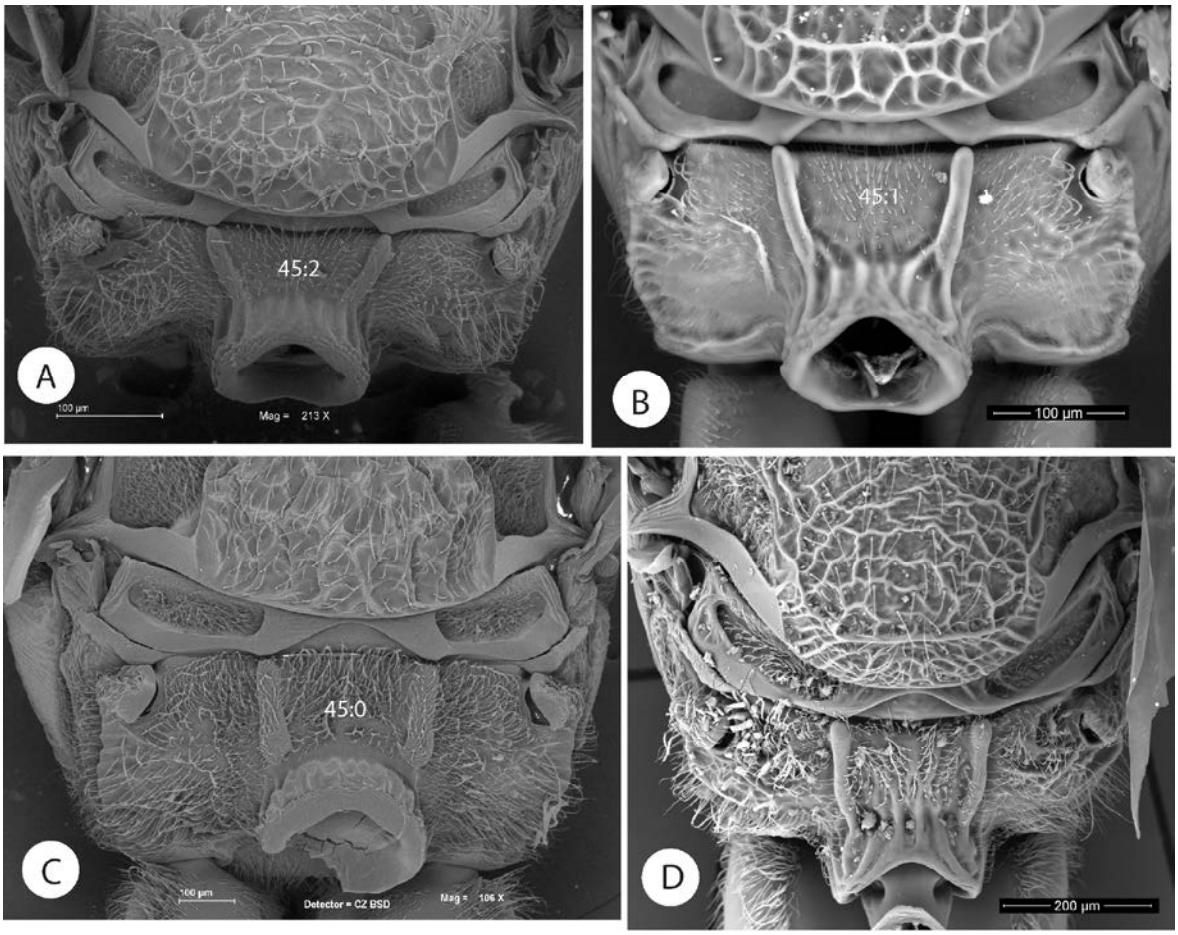

Figure 12. Propodeum posterior view of *Synergus* species: (A) *Synergus chiricanus*. (B) *Synergus gabrieli.* (C) *Synergus nicaraguensis*. (D) *Synergus ramoni.*

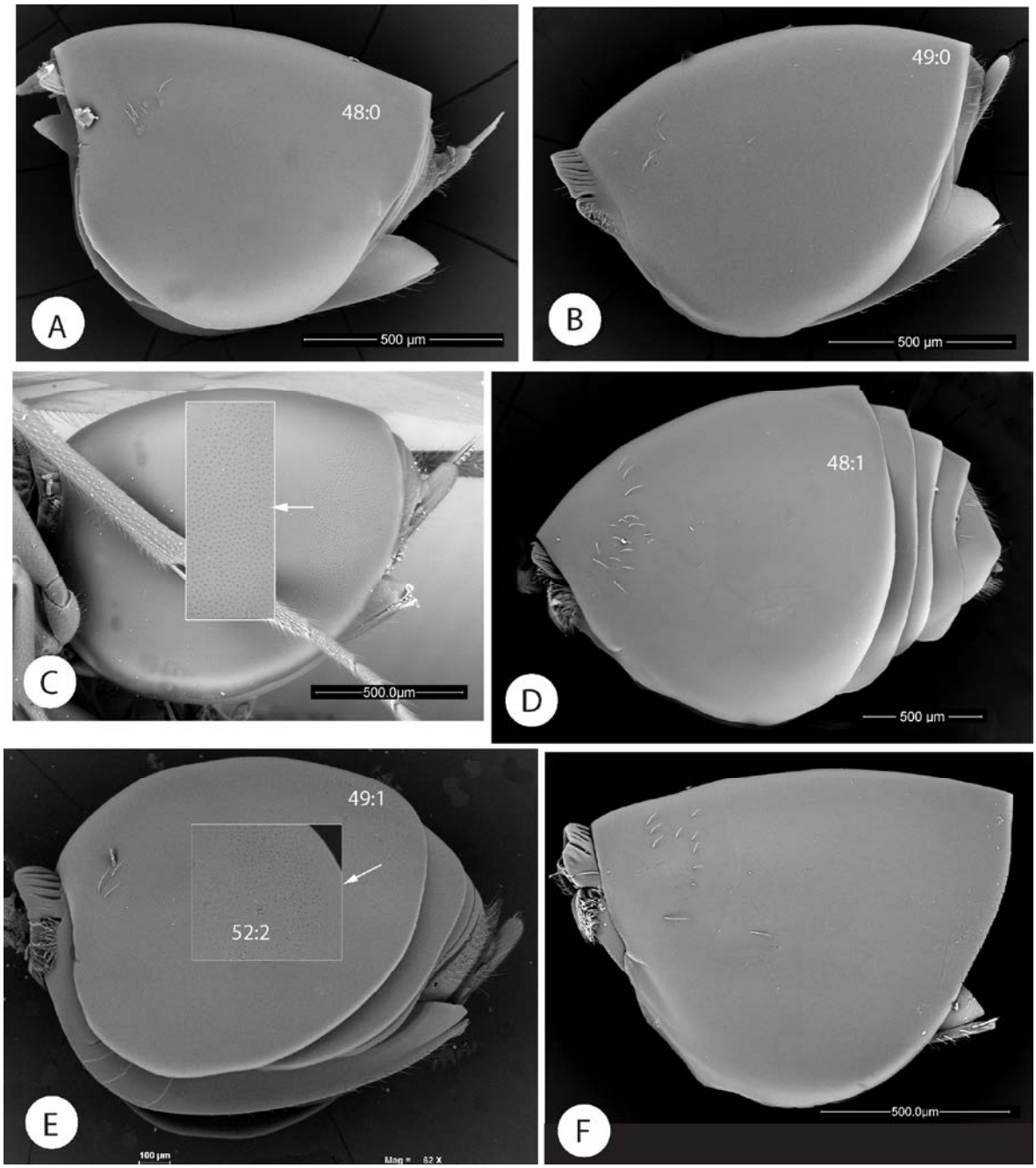

Figure 13. Metasoma lateral view of *Synergus* species: (A) *Synergus elegans*. (B) *Synergus laticephalus*. (C) *Synergus rufinotaulis*. (D) *Synergus mesoamericanus*. (E) *Synergus nicaraguensis*. (F) *Synergus ramoni*.

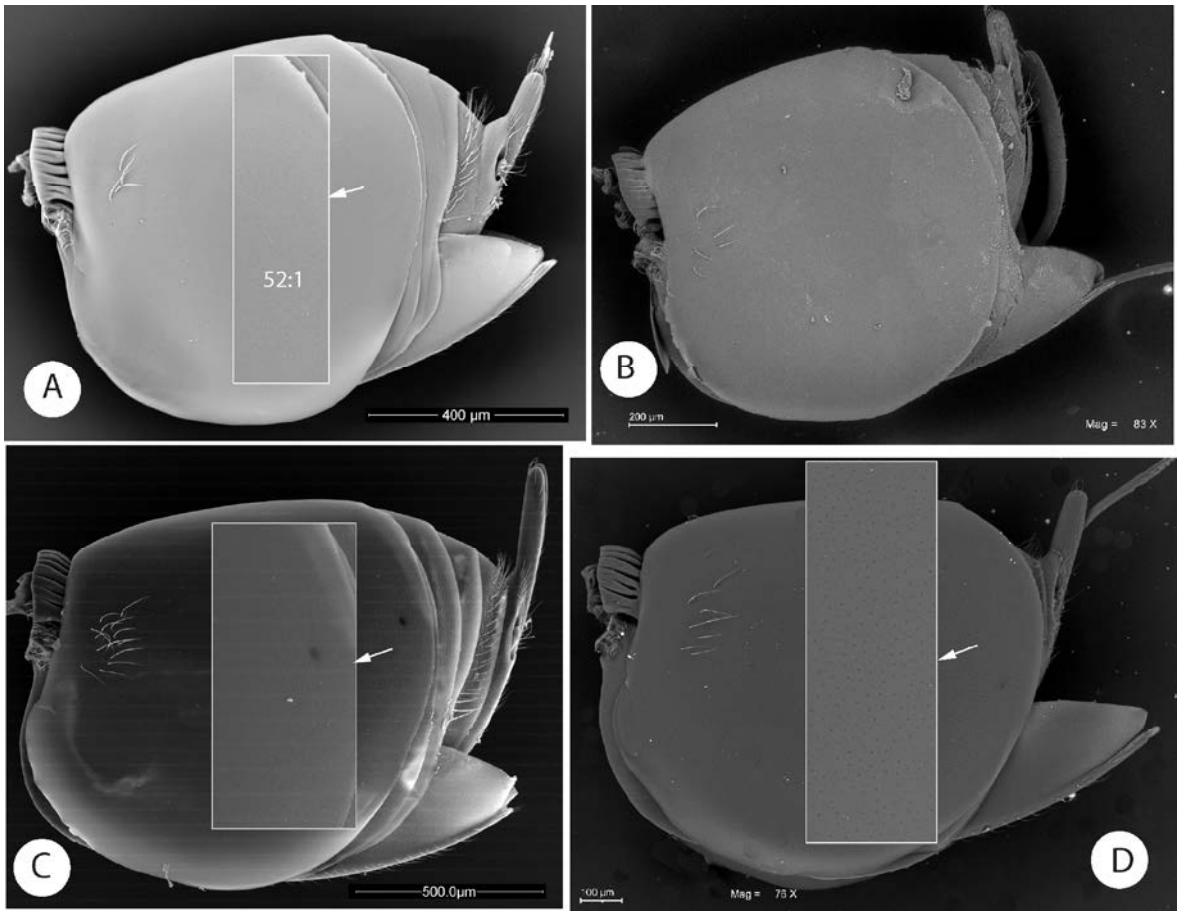

Figure 14. Metasoma lateral view of *Synergus* species: (A) *Synergus gabrieli*. (B) *Synergus chiricanus*. (C) *Synergus baruensis*. (D) *Synergus luteus*.

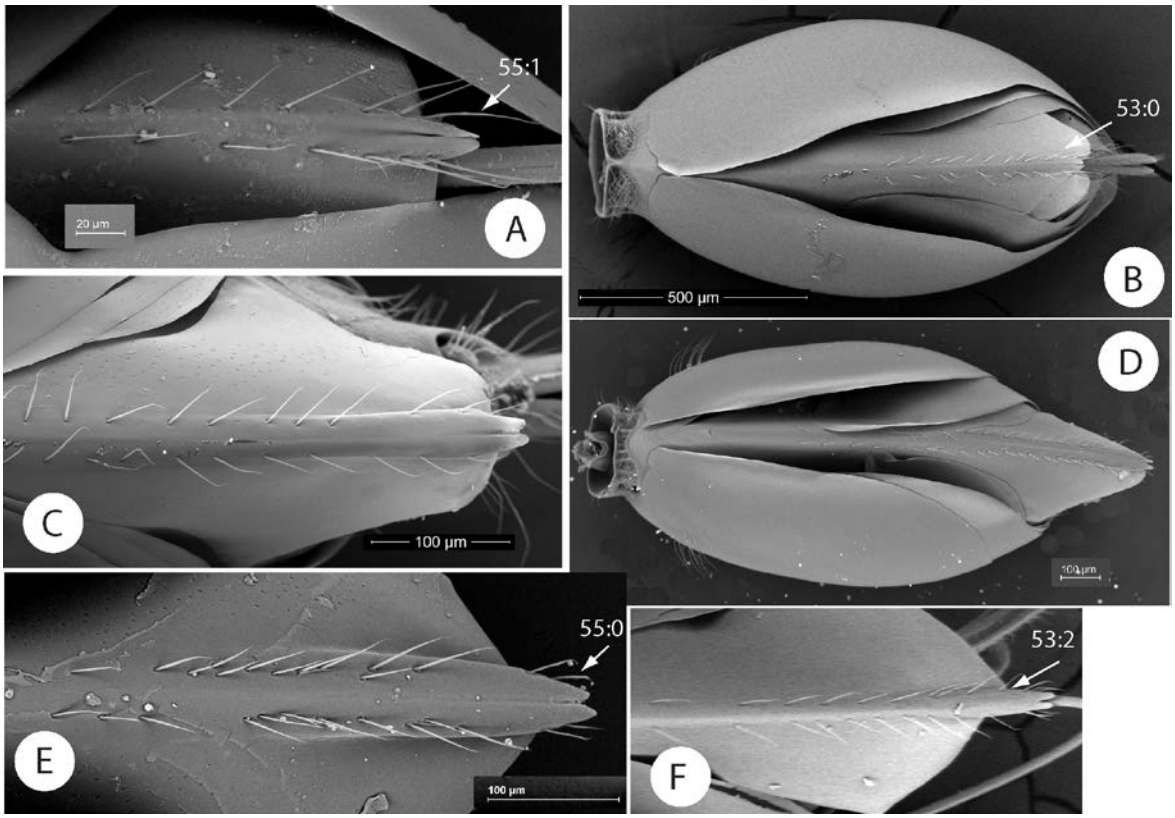

Figure 15. Hypopygium ventral view of *Synergus* species: (A) *Synergus elegans*. (B) *Synergus laticephalus*. (C) *Synergus gabrieli*. (D) *Synergus luteus*. (E) *Synergus nicaraguensis*. (F) *Synergus mesoamericanus*.

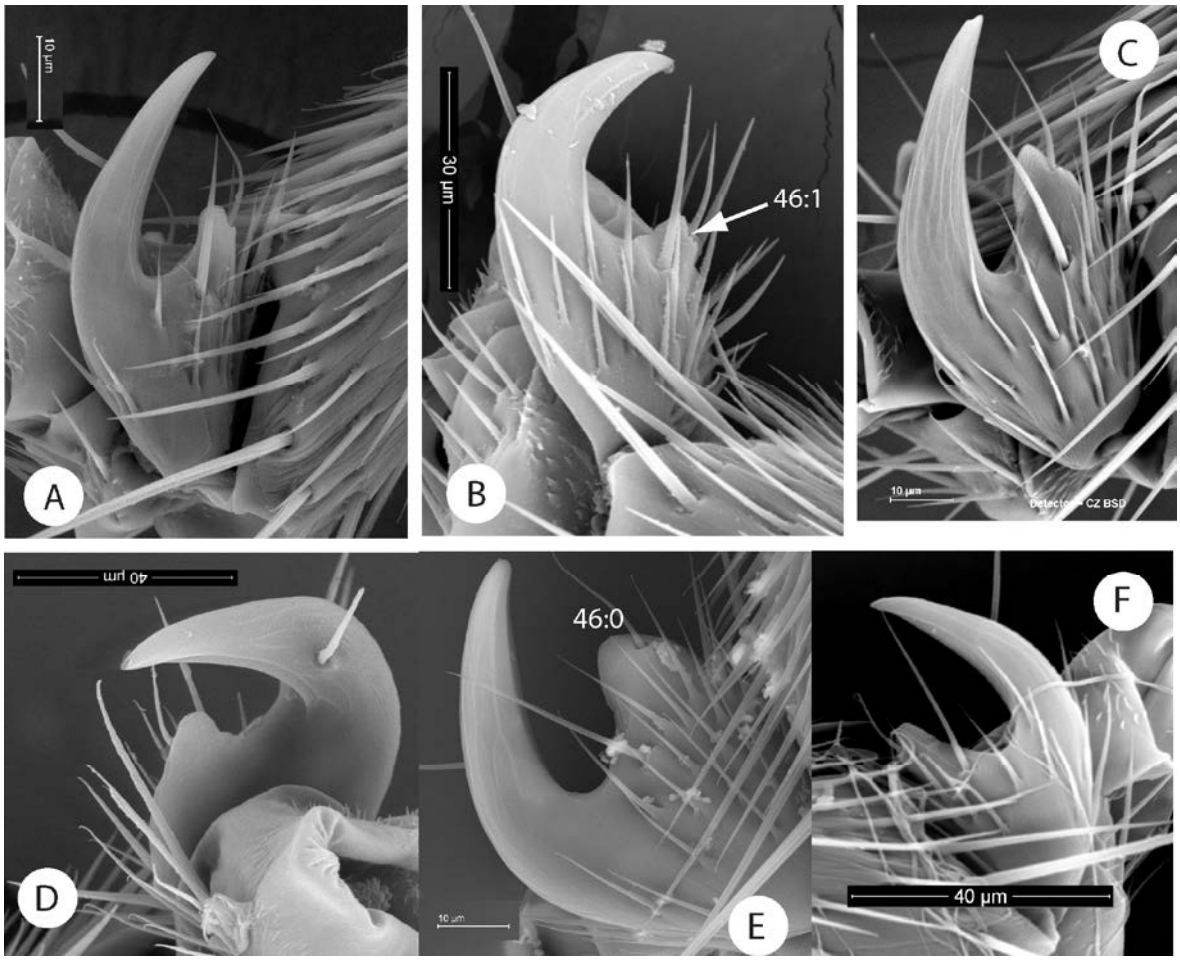

Figure 16. Metatarsal claws of *Synergus* species: (A) *Synergus elegans*. (B) *Synergus ramoni*. (C) *Synergus nicaraguensis*. (D) *Synergus mesoamericanus*. (E) *Synergus luteus*. (F) *Synergus gabrieli*.

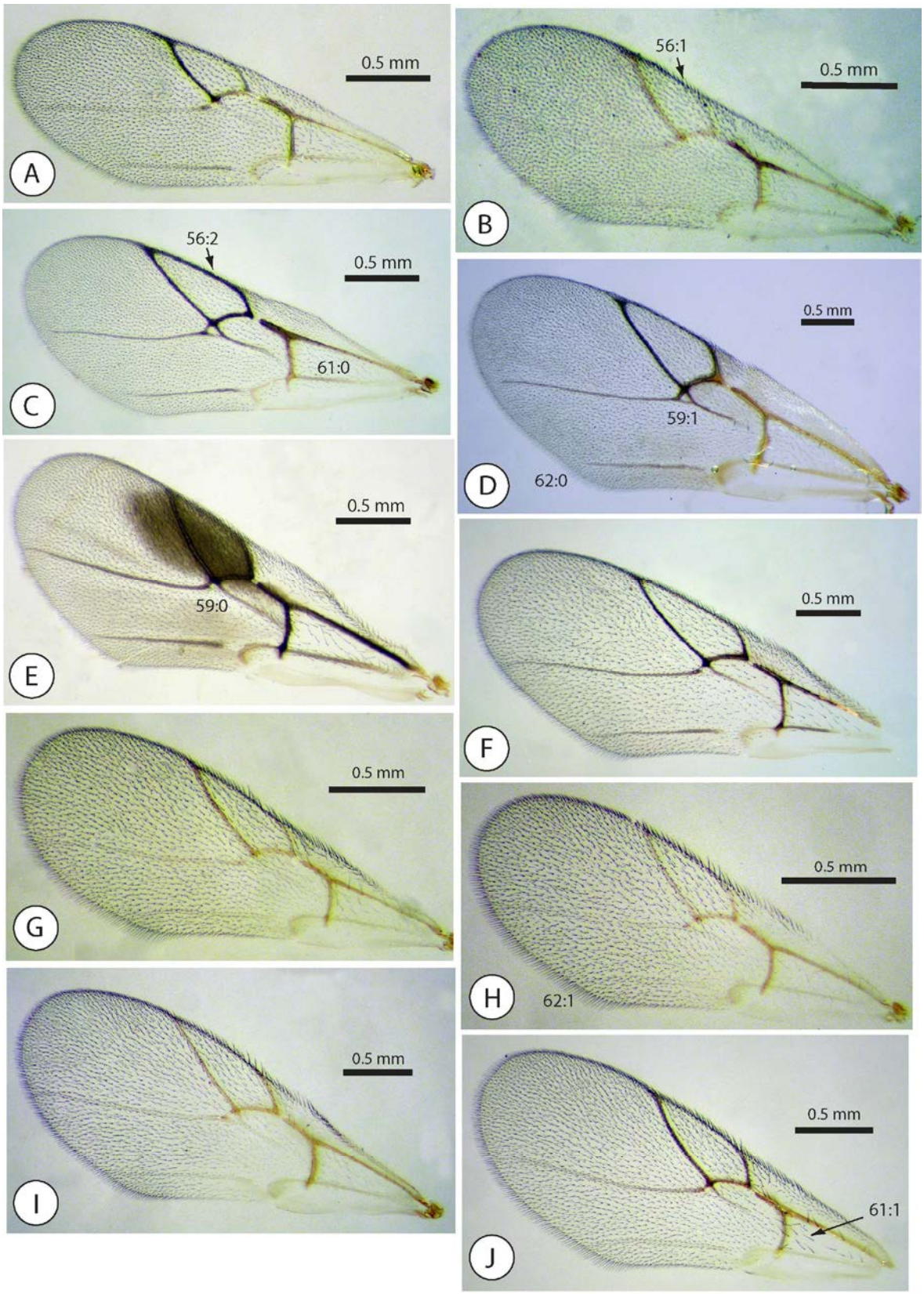

Figure 17. Forewing of *Synergus* species: (A) *Synergus laticephalus*. (B) *Synergus elegans*. (C) *Synergus ramoni* (D) *Synergus mesoamericanus*. (E) *Synergus nicaraguensis*. (F) *Synergus rufinotaulis*. (G) *Synergus gabrieli*. (H) *Synergus chiricanus*. (I) *Synergus luteus*. (J) *Synergus baruensis*.

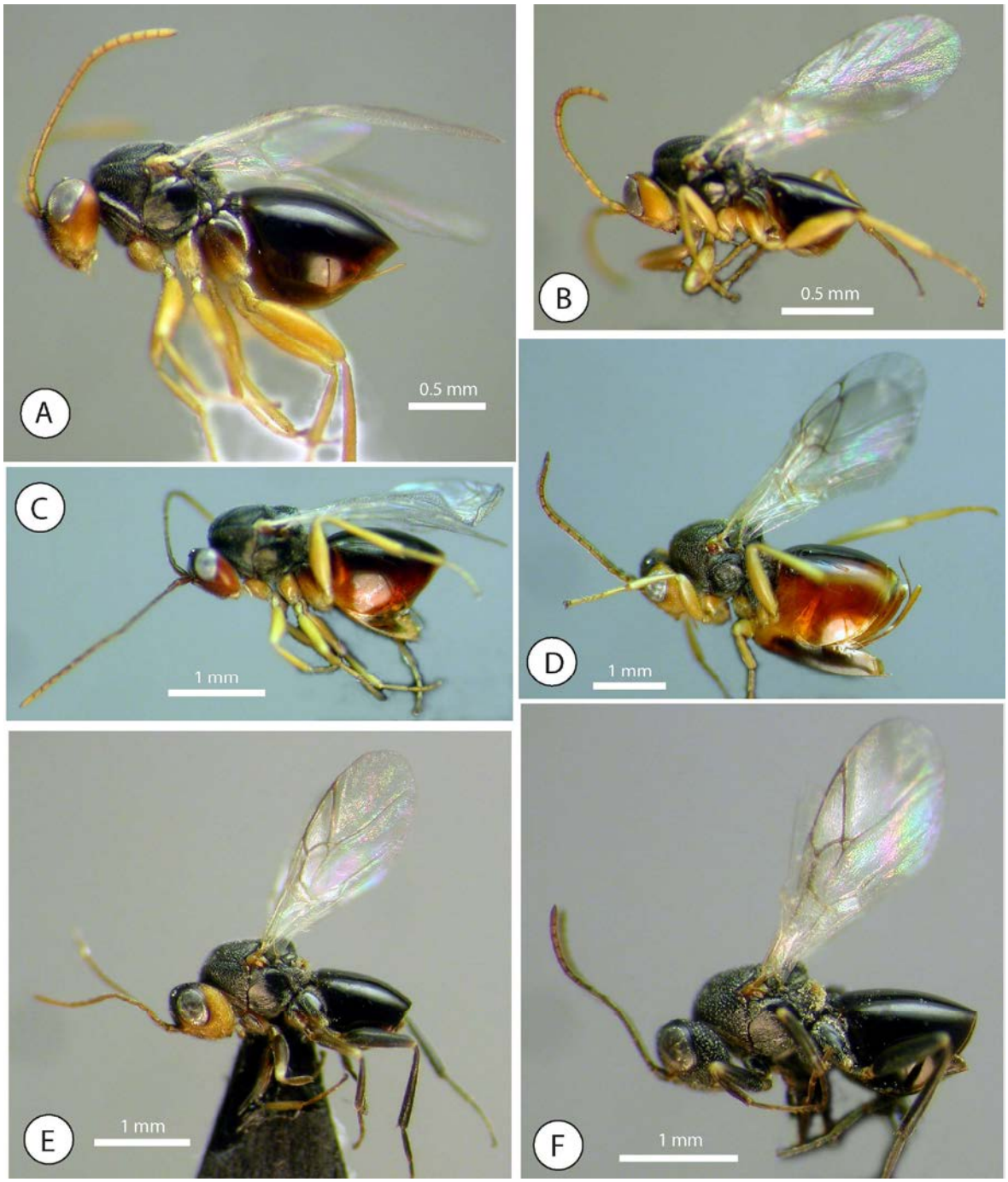

Figure 18. Habitus of *Synergus* species: (A) *Synergus elegans,* female. (B) *Synergus elegans,* male. (C) *Synergus laticephalus,* female. (D) *Synergus mesoamericanus*, female (E) *Synergus ramoni*, male. (F) *Synergus ramoni*, female.

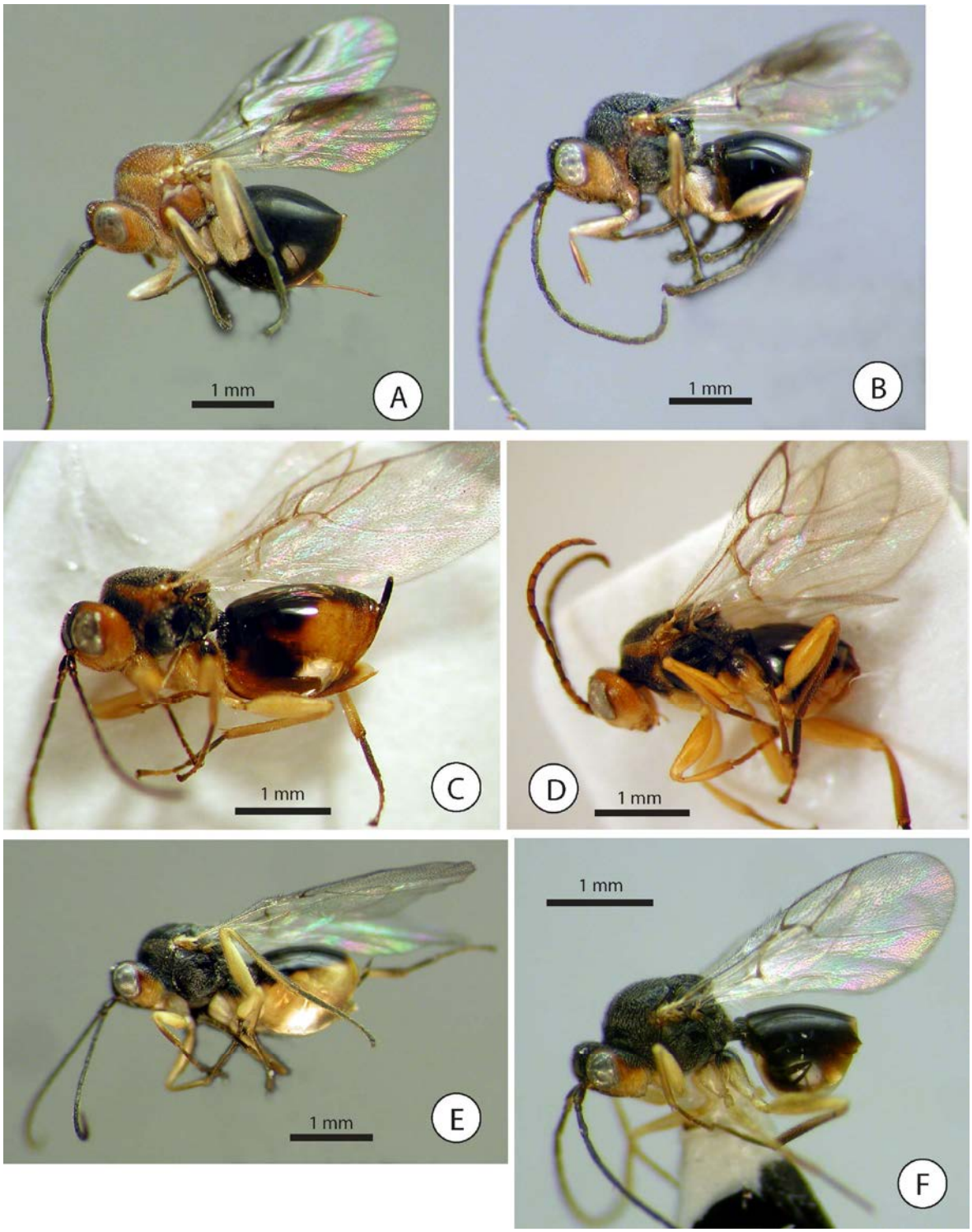

Figure 19. Habitus of *Synergus* species: (A) *Synergus nicaraguensis*, female. (B) *Synergus nicaraguensis*, male. (C) *Synergus colombianus*, female. (D) *Synergus colombianus*, male. (E) *Synergus rufinotaulis*, female. (F) *Synergus rufinotaulis*, male.

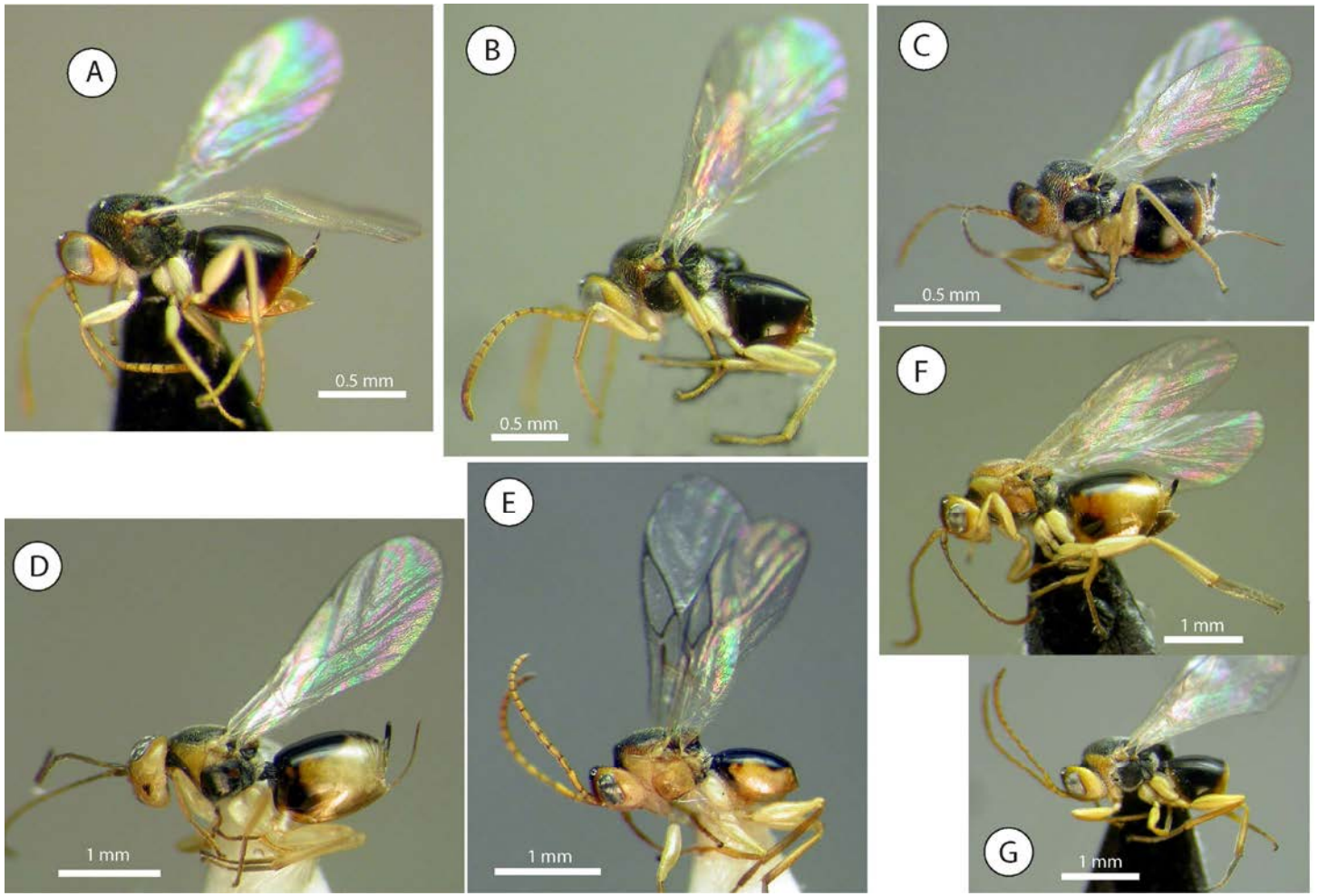

Figure 20. Habitus of *Synergus* species: (A) *Synergus gabrieli*, female. (B) *Synergus gabrieli*, male. (C) *Synergus chiricanus*, female. (D) *Synergus baruensis*, female. (E) *Synergus baruensis*, male. (F) *Synergus luteus*, female. (G) *Synergus luteus*, male.

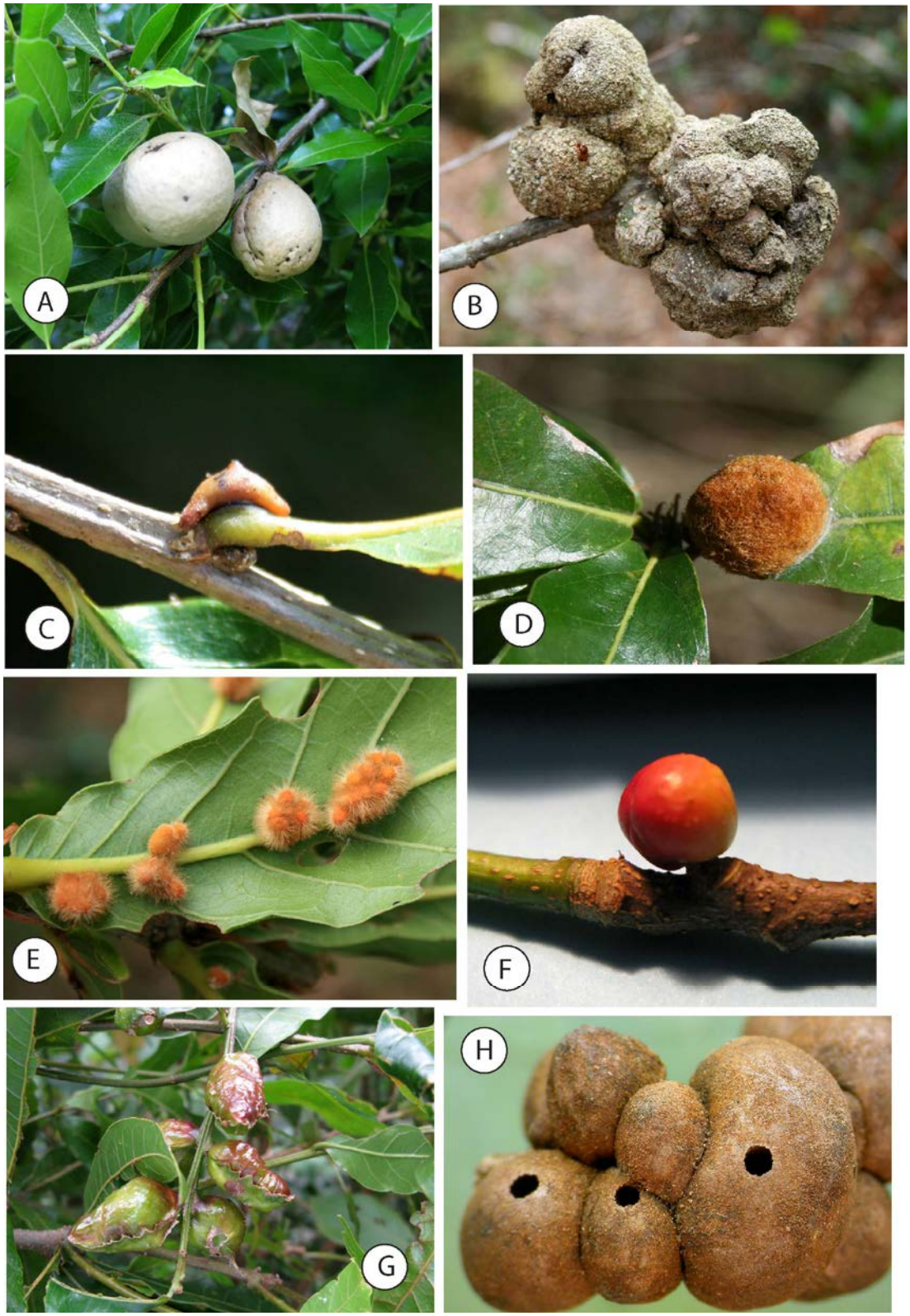

Figure 21. Host galls of *Synergus* species from Panama: (A) *Amphibolips castroviejoi.* (B) *Andricus championi.* (C) *Trigonaspis sp. indet.*, female?. (D) *Andricus guatemalensis*. (E) *Neuroterus sp. nov.* (F) *gen. sp. indet.* (G) *Callirhytis sp. nov.* (H) *Disholcaspis sp. nov*.

Figure 22. Host galls of *Synergus* species from Panama: (A) unidentified cynipid genus on twigs of *Quercus salicifolia*, (B) undescribed species of *Loxaulus* or *Bassettia* genera on *Quercus bumelioides*, (C) gall of an unidentified genus, (D) *Cynips sp. nov.*, (E) *Neuroterus sp. nov*., (F) *Cynips sp. nov*., (G) unidentified cynipid genus on *Quercus salicifolia*.

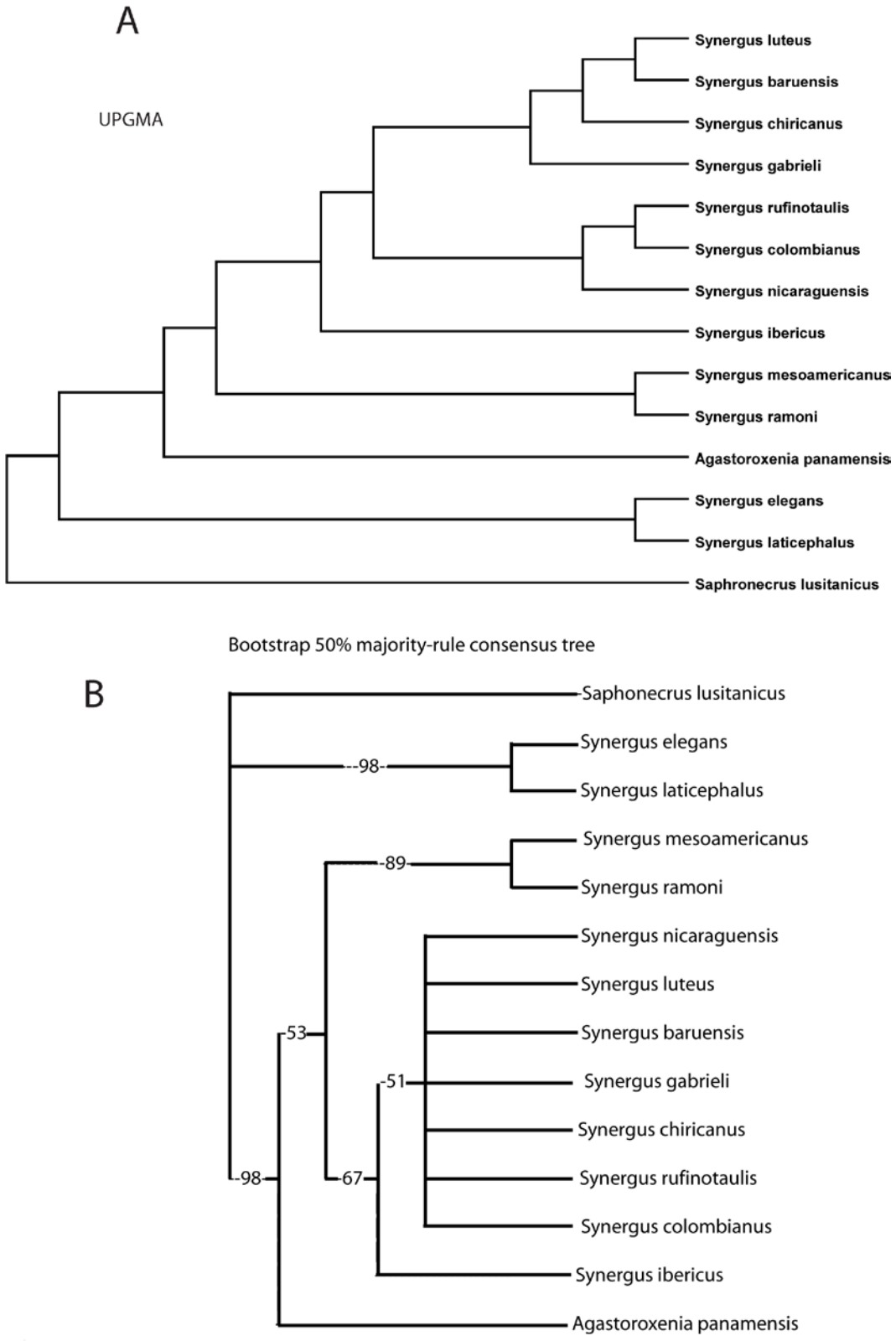

Figure 23. Resulting trees of the morphological phylogenetic analysis. (A) Overall similarity phenogram of a UPGMA tree (cluster analysis, unweighted pair group method analysis). (B) strict consensus tree of the shortest trees resulting from heuristic analysis of the complete dataset, bootstrap support indicated.

DISCUSIÓN GENERAL

Logros y limitaciones taxonómicas de esta investigación

Los resultados que se recogen en esta tesis representan un avance significativo en el conocimiento de la Taxonomía y Sistemática de la familia Cynipidae en la república de Panamá, América Central y el conjunto de la región neotropical, áreas geográficas, todas ellas, muy deficientemente conocidas hasta el momento en lo que se refiere a la fauna de los cinípidos. De la singularidad de la fauna panameña de cinípidos y su déficit de estudio dan buena prueba las 17 especies nuevas para la ciencia descritas como resultado de esta investigación. Hay que hacer énfasis, sin embargo, en que la fauna que se ha podido estudiar en profundidad, en la que se incluyen las nuevas especies descritas, es sólo una fracción del conjunto del material colectado de cinípidos y, aún menor de la diversidad real estimada de Cynipidae en el área estudiada. Las limitaciones de tiempo y recursos que plantea una investigación doctoral han hecho imposible abarcar el estudio de todo el material colectado. Quedan por estudiar los géneros de la tribu Cynipini más ricos en especies y también más complejos en el aspecto taxonómico, como son los géneros *Andricus, Cynips, Neuroterus* y *Callirhytis* que requieren todos ellos de una exhaustiva y cuidadosa revisión para poder llegar a conclusiones definitivas sobre el estatus de las especies estudiadas y la descripción de las probables especies nuevas. Por ejemplo solo del género *Andricus*, que en cuanto a riqueza específica es el género de cinípidos mejor representado en las muestras que hemos colectado en Panamá, hay citadas unas 140 especies, distribuidas desde Canadá hasta México. Del género *Neuroterus*, el segundo con más especies en Panamá, se han citado más de 80 especies en Norteamérica (Burks, 1979; Pujade-Villar *et al.,* 2009).

Otro de los problemas en la taxonomía de los Cynipidae neárticos y neotropicales, como ya se ha discutido en los manuscritos correspondientes a los géneros *Bassettia* y *Ondontocynips,* es el de la definición imprecisa de los límites entre algunos géneros endémicos de las dos regiones biogeográficas, con otros géneros de distribución geográfica más amplia. Esto ha hecho difícil la correcta adscripción genérica de algunas especies nuevas encontradas en nuestro estudio, ya que su estudio preliminar indica que encajan con dificultad en géneros actuales y pudieran necesitar la descripción de nuevos géneros para su correcta clasificación. Esta decisión requiere, sin embargo, de cuidadosa revisión del material tipo y otras especies además de consulta con otros especialistas, por lo que estos resultados no han podido ser incluidos en esta memoria y necesitarán más tiempo para su finalización.

La escasez u obsolescencia de las claves de identificación a nivel de género y la práctica ausencia de las claves de identificación de especies son uno de los mayores impedimentos en el progreso de la taxonomía de los Cynipidae de América. Hay que recurrir por ello con frecuencia a las descripciones originales que son por lo general insuficientes para la correcta diferenciación entre especies afines. Los trabajos generales que incluyen una revisión de la familia Cynipidae a nivel mundial como el de Dalla Torre & Kieffer (1910) y Weld (1952), se encuentran desfasados, tanto a nivel de géneros como de especies, frente a la información de los cinípidos que se ha generado en las ultimas décadas. Como se menciona en el primer manuscrito de esta memoria (capítulo 1.1) la más reciente revisión de los géneros de la tribu Cynipini realizada por Melika & Abrahamson (2002) hay que utilizarla con muchas reservas ya que muchos de las sinonimias, nuevas combinaciones y otros actos nomenclaturales realizados en el mencionado trabajo han resultado erróneos a la luz de recientes investigaciones (ver Liljeblad *et al.,* 2008; Pujade-Villar, 2010; Melika *et al.,* 2010). La opinión general de los diferentes especialistas estudiosos de los cinípidos inductores de agallas en robles es que la fauna de la región Neártica (que es la principal referencia de la de Centroamérica y Colombia) necesita ser revisada, ya que muchos de los nombres genéricos que se han utilizado para incluir las especies de esta región no guardan relación con los taxones de nivel género de la región Paleartica donde fueron originalmente descritos (Nieves-Aldrey *com. pers*.; Melika *com. pers*). La tarea que queda por realizar en los siguientes años será, por tanto, ardua y laboriosa hasta que la fauna de cinípidos colectada en Panamá sea completamente revisada y descrita. Esta tarea incluirá recuperar de las agallas el porcentaje de los adultos inductores que no se ha conseguido en los muestreos de este estudio, intentar esclarecer los ciclos heterogónicos de las especies, poniendo en correspondencia los pares de generaciones sexuales / asexuales de las especies encontradas, describir los nuevos géneros claramente identificados por sinapomorfias y proporcionar unas claves generales de la fauna panameña de Cynipidae. En la tarea de construir una clasificación natural de los cinípidos de Panamá y neotropicales seran de gran ayuda los estudios de filogenia molecular y filogeografía sobre Cynipidae actualmente en marcha (Stone *et al*., 2009; en prep.) Igualmente las especies de los cinco géneros de la tribu Cynipini que se abordan en esta tesis; *Amphibolips*, *Bassettia*, *Disholcaspis*, *Loxaulus* y *Odontocynips*, al tener su distribución restringida en América nos permiten realizar inferencias biogeográficas de los Cynipidae en este continente y

completar a corto y mediano plazo estudios de Filogeografía con un grupo de colegas mexicanos que en este momento se encuentra desarrollando investigación sobre el mismo tema.

Aspectos biogeográficos de la fauna de los cinípidos de Panamá

Los resultados obtenidos en este trabajo, que constituyen la base de partida para futuras investigaciones en toda la región Neotropical, nos permitirán plantear y testar en el futuro hipótesis biogeográficas sobre el origen de la fauna de cinípidos de Panama. Hoy podemos afirmar que como consecuencia del levantamiento y cierre del Istmo de Panamá, que culminó hace aproximadamente 3.5 millones de años y que provocó que se estableciera un corredor montañoso que conectó la Sierra Madre del Sur de México con las cordilleras de Centroamérica y los Andes Suramericanos (Samudio Jr., 2001 y referencias allí citadas), un considerable número de especies de cinípidos inductores de agalla de la tribu Cyninipi y sus inquilinos de la tribu Synergini se distribuyeron a través de toda la región centroamericana siguiendo la distribución de sus plantas hospedantes, y formando parte de lo que se ha denominado el gran intercambio biótico americano (Stehli & Webb, 1985). Según Hooghiemstra (2006) las especies de *Quercus* emigraron desde Norteamérica hasta los andes colombianos durante el Neógeno y Pleistoceno en los periodos glaciares e interglaciares. De acuerdo a diferente fuentes el género *Quercus* que es considerado un inmigrante reciente en los Andes Suramericanos (Colombia) llegó hace unos 250.000 o 340.000 años a las sabanas de Satafé de Bogota (van der Hammen & Gonzales, 1963; Hooghiemstra & Sarmiento, 1991; Kappelle, 1996), lo que nos podría dar una idea mínima de la antigüedad de las poblaciones de Cynipidae en Panamá, ya que la llegada de este género de plantas hasta Colombia es un efecto directo del surgimiento del istmo panameño y los periodos glaciares por los que atravesó el planeta. Esta misma confirmación nos plantea una serie de hipótesis que tendrán que ser comprobadas con futuras investigaciones sobre como ocurrió el desplazamiento de los Cynipidae a través de Centroamérica. De acuerdo a las teorías actuales (Stone *et al.,* 2009) los herbívoros siguiendo la distribución de su hospedador presentan tres comportamientos; 1) la radiación evolutiva se produce al tiempo que la de su planta hospedante en cuyo caso la filogenia de plantas y herbívoros sería concordante 2) se produce poco después que se ha producido en sus plantas hospedantes (hipótesis de la colonización rápida) o 3) mucho tiempo después de la diversificación de las plantas

(hipótesis de la colonización tardía). Dilucidar que mecanismos de radiación evolutiva y colonización se produjeron en el caso de los cinípidos en Centroamérica servirá para comprender mejor la filogenia del grupo y entender por ejemplo problemas concretos como el de los rasgos morfológicos aberrantes y/o peculiares encontrados en algunas especies no identificadas encontrados en sitios tan aislados como la cima del Volcán Barú a 3475 m.s.n.m, explicando si son de reciente especiación o constituyen fósiles vivientes.

Especificidad con la planta hospedante

Según Stone *et al.* (2009), Melika *et al*. (2010), existe una profunda división evolutiva entre los géneros de cinípidos inductores de agallas basada en las diferentes secciones del subgénero *Quercus* al que pertenece su especie hospedante. Las primeras evidencias generadas de este nuestro estudio parecen apoyar esta hipótesis ya que los resultados indican que un mayor número de géneros y especies de cinípidos inductores de agalla en Panamá están relacionados con especies de la sección *Quercus* (robles blancos) que con la sección Lobatae (robles rojos), puesto que de las 65 morfotipos de agallas de cinípidos colectados en Panamá solo 14 estuvieron relacionados con la sección Lobatae, principalmente a *Quercus salicifolia,* o lo que Nixon (2006) denomina el complejo *seemanni*. Estos resultados son congruentes con lo que se observa en la fauna Paleártica con respecto a las faunas de cinípidos asociadas a la sección Quercus y a las secciones Cerris e Ilex, estas dos últimas también con faunas minoritarias con respecto a la fauna de cinípidos asociada a la sección Quercus.

Diversidad de las avispas inductoras de agallas en los robles de la región Neotropical

Nuestro resultados sugieren que, a diferencia de lo documentado antes de iniciar este estudio, la región Neotropical alberga una rica fauna de cinípidos inductores de agallas en robles, y que los escasos registros que se tiene de la familia en el Neotrópico se deben básicamente a falta de muestreos en la región y no a la ausencia de la familia en la misma. En efecto, si en Panamá, donde la fauna de cinípidos probablemente este depauperada por efectos de ser este país el límite de la distribución de los *Quercus,* se han encontrado 65 especies de agallas sobre seis especies de *Quercus,* en el resto de Centroamerica, donde se estima se encuentran cerca de 35 especies de *Quercus*

(Valencia-A, 2004), deben existir un número aún más importante de cinípidos inductores de agallas de la tribu Cynipini, tal como postuló Kinsey (1936).

Diversidad de cinípidos inquilinos neotropicales

Las especies inquilinas de la tribu Synergini merecen un comentario aparte. Es de destacar el hallazgo de un género nuevo de inquilino, que es el primero de este grupo trófico que se describe en la región neotropical. La fauna de inquilinos del género *Synergus* es sorprendentemente rica en Panamá, como demuestra la descripción de ocho nuevas especies para la ciencia de dicho género, y a tenor del material adicional encontrado, aún en periodo de estudio, futuros trabajos pueden demostrar que la fauna de inquilinos es incluso más rica. La variación morfológica encontrada dentro del género *Synergus* en el análisis filogenético efectuado, que cuestiona la monofilia de las especies de Panamá (ver artículo correspondiente a las especies de inquilinos de Panamá) puede hacer replantearse en el futuro la clasificación de las especies del género, pero habrá que esperar a que nuevas evidencias moleculares confirmen o no los resultados basados en morfología. La incongruencia se refiere a especies como *Synergus elegans* y *S. laticephalus* que por su posición filogenética en el analisis realizado podrían precisar la descripción de un nuevo género que las agrupe. Por otro lado, se confirman observaciones realizadas por Nieves-Aldrey (2005) con referencia a la importancia del carácter de la carena lateral del pronoto en la taxonomía de las especies de *Synergus*, la cual está ausente en todas las especies conocidas de la región neotropical, mientras que está presente en la mayoría de las especies paleárticas, con excepción de unas pocas especies de posición basal en el árbol filogenético del grupo.

Aspectos morfológicos aportados en el estudio

Los resultados que presentamos en este estudio contribuyen a la mejor definición morfológica de cada uno de los géneros de inductores de la tribu Cynipini y las especies inquilinas de la tribu Synergini. En todos los casos las especies encontradas en Panamá presentaron uno o un conjunto de estados de caracteres morfológicos que esperamos ayuden a definir mejor los límites de los géneros incluidos en esta tesis. En el caso de los cinco géneros de inductores estudiados los datos confirman, como ya había sido mencionado por Nieves-Aldrey (1992), que la presencia o no de un segundo diente o lóbulo en la uña metatarsal es una homoplasia que no ayuda a definir géneros dentro de

la tribu Cynipini. Los caracteres en los que nos hemos basado para incluir las especies en los diferentes géneros son la presencia y la forma de las carenas laterales y medial del propodeo, la forma y longitud de la espina ventral del hipopigio, así con la presencia, longitud y disposición de las setas que se encuentra en dicha espina hipopigial. Caracteres como la escultura del mesosoma *e.j.* fuertemente rugosos en los *Amphibolips*, finamente coriaceo en *Loxaulus* o fuertemente estriado en *Bassettia* son de gran utilidad en la definición a nivel genérico de las especies. La presencia o ausencia de un surco sub-ocular o malar, la forma del mesosoma *e.j* deprimido dorso-ventralmente en las especies de *Bassettia* y *Loxaulus* o tan alto como largo en los *Amphibolips y Disholcaspis,* así como la presencia, forma, profundidad y esculturación de las fosetas escutelares son útiles para complementar la definición genérica de las especies. Otros caracteres como la anchura de la cabeza con respecto a la del mesosoma o la relación de la longitud de los primeros flagelómeros con los últimos en la antena ayuda a identificar especies de los géneros *Loxaulus*, *Bassettia* y *Disholcaspis*. Caracteres como el lóbulo romo en el fémur de la pata posterior que define al género *Odontocynips* deberá ser estudiado más a profundidad para determinar si el mismo es realmente una sinapomorfia o una homoplasia como se discute en el artículo de las especies de este género encontradas en Panamá. Sin lugar a dudas todas las características referentes a la agalla que induce cada una de las especies de Cynipini al igual que la sección del género *Quercus* al que pertenece su hospedador es un apoyo trascendental en la ubicación genérica de la especie.

Importancia de los cinípidos en la conservación de los bosques montanos de Panamá

Debido a que la mayor parte de las especies de *Quercus* en Centroamerica (*Q. oleoides* es la excepción) se distribuyen en las tierras altas de esta región estas plantas forman parte de los denominados bosque nublados montanos tropicales. Los bosques nublados montanos tropicales (bosques nubosos) representan un raro y frágil ecosistema que está bajo amenaza en muchas partes del mundo. En Panamá la fauna de cinípidos encontrada durante este estudio esta ligada inevitablemente a las poblaciones de *Quercus*, las cuales se encuentran altitudinalmente muy aisladas (entre 1000-3100 m), y fragmentadas debido a las actividades agropecuarias que se desarrollan en estas áreas, y a la creciente degradación y sustitución de los bosques montanos de *Quercus* por

cultivos u otras formaciones vegetales. Un elemento adicional que complica la situación de las poblaciones de *Quercus* y cinípidos en Panamá son los efectos del llamado calentamiento global, ya que estudios con polen realizados en la cordillera del Talamanca en Costa Rica indican que durante los últimos 18.000 años los bosques de *Quercus* se han desplazado a diferentes alturas en busca de las condiciones climáticas (principalmente temperatura) apropiadas para su desarrollo (Kappelle, 1996). Como en Panamá las poblaciones de *Quercus* crecen en los sitios de mayor altitud, cualquier aumento en la temperatura actual de la zona donde crecen estos árboles se convertiría en un factor limitante para el desarrollo de dichas especies arbóreas, lo que traería como consecuencia la pérdida de la mayor parte de la fauna asociada a estas especies incluyendo los cinípidos.

Futuros estudios

Los resultados obtenidos en esta tesis, que han superado nuestras expectativas en cuando a la riqueza de especies e interacciones biológicas y evolutivas, que "a priori" habíamos imaginado, nos abre un amplio abanico de futuras líneas de investigación en diferentes campos como la Sistemática, Morfología, Biología, Ecología, Etología, Filogenia y Filogeografía, que intentaran ser abordados con las posibilidades de futuros recursos con los que se cuente o se puedan obtener. De igual manera este trabajo es el inicio de subsiguientes investigaciones sobre el tema en países vecinos como Colombia, Costa Rica y El Salvador donde ya existe el interés de otros investigadores de contribuir al conocimiento de este grupo de insectos, tan interesantes por tantos conceptos, y que se puede considerar que están en el punto más alto en la evolución de la fitofagia al conjugar el hecho de la inducción de las zoocecidias más complejas, con la peculiaridad de que éstas constituyan un recurso que sustenta una multitud de otras interacciones tróficas y ecológicas, casi todas aún por desvelar en la fauna neotropical.

CONCLUSIONES

1. Se ha realizado por primera vez un estudio sistemático de la fauna de cinípidos inductores de agallas (Cynipidae: Cynipini) y sus comunidades de inquilinos (Cynipidae: Synergini) asociados a las especies de *Quercus* de Panamá un país centroamericano incluido en la región neotropical.
2. Las tierras altas de Panamá albergan una alta riqueza de géneros y especies tanto de cinípidos inductores de agallas como de inquilinos. Se han contabilizado 65 morfotipos de agallas de especies de cinípidos englobadas en 12 géneros de cinípidos inductores de agallas, dos de los cuales corresponden a géneros no descritos.
3. Se aporta una lista de 21 especies de la familia Cynipidae citadas para Panamá, de las cuales 10 son inductores de agallas y 11 son inquilinas. Estas cifras contrastan con la única especie que había sido citada previamente de Panamá.
4. La fauna actual en el Neotrópico de la familia Cynipidae queda constituida por seis tribus, 18 géneros y 45 especies, 41 de las cuales son nativas y cuatro han sido introducidas en la región.
5. *Andricus, Neuroterus* y *Dryocosmus* son los géneros de la tribu Cynipini representados por mayor número de especies en Panamá.
6. Se revisan taxonómicamente las especies de los géneros *Amphibolips*, *Disholcaspis*, *Loxaulus*, *Bassettia* y *Odontocynips* (Cynipidae: Cynipini) de Panamá. Se describe la morfología de todas las especies, se aportan claves de identificación y se dan datos de biología de todas las especies.
7. Se describen ocho nuevas especies para la ciencia de la tribu Cynipini: *Amphibolips castroviejoi, A. aliciae, A. salicifoliae, Disholcaspis bettyannae, Disholcaspis bisethiae, Loxaulus panamensis, Loxaulus championi y Bassettia caulicola,* se describen por primera vez los adultos de *Odontocynips championi* y se asigna un Neotipo para esta especie. Se amplia el área de distribución de *Odontocynips hansoni*, citándola en Panamá.
8. Se revisa taxonómicamente la fauna de cinípidos inquilinos de Panama. La fauna queda integrada por dos géneros y 11 especies. Previamente no se había citado ninguna especie del grupo en Panamá.
9. Se describe un género nuevo y especie de inquilinos de la tribu Synergini. *Agastoroxenia panamensis* Nieves-Aldrey & Medianero, 2010.

10. Se describen ocho nuevas especies para la ciencia de inquilinos del género Synergus: *Synergus elegans, S. laticephalus, S. ramoni, S. rufinotaulis, S. luteus, S. gabrieli, S. baruensis y S. chiricanus*. Dos especies*: S. mesoamericanus* y *S. nicaraguensis* conocidos de Guatemala y Nicaragua se citan por primera vez para Panamá.
11. Se efectúa el primer análisis filogenético basado en caracteres morfológicos de especies de cinípidos inquilinos. El análisis incluyó los dos géneros y 11 especies encontradas en Panamá, con representantes como grupos externos de otros géneros y especies de la fauna paleártica y neotropical. El análisis se basó en 65 caracteres, 62 de morfología externa del adulto y tres caracteres de biología.
12. El análisis filogenético realizado con las especies de inquilinos establece tres grupos monofileticos bien soportados; uno constituido por las especies *S. elegans* y *S. laticephalus* que están próximas a *Saphonecrus lusitanicus,* otro compuesto por *Agastoroxenia* como grupo hermano de las demás especies de *Synergus* de Panamá que incluye las especie Paleartica *S. ibericus* y un tercer clado monofiletico compuesto por *S. mesoamericanus* y la nueva especie descrita *S. ramoni.*
13. Como consecuencia del estudio de los Cynipidae de Panamá se concluye que por extensión, la fauna de cinípidos de las regiones neártica y neotropical requieren revisiones exhaustivas, en particular para una mejor definición de los límites al nivel taxonómico de género.
14. Las especies inductoras de agallas de Panamá están más asociadas a especies de la sección Quercus que a especies de la sección Lobatae del subgénero *Quercus*.
15. En Panamá *Quercus bumelioides* es la especie que sirve de hospedador a un mayor número de especies de cinípidos inductores de agallas, seguida por *Q. lancifolia* y *Q. salicifolia.*
16. Las agallas encontradas son mayoritariamente inducidas en hojas y con la excepción de las inducidas por las especies de los géneros *Amphibolips* y *Disholcaspis* no presentan estructuras morfológicas externas sofisticadas, o asociaciones con hormigas, pero mantienen una rica fauna asociada de parasitoides.

17. La riqueza y composición de especies de la fauna de cinípidos asociada a *Quercus* de Panamá es la consecuencia de episodios de colonización y recolonización, a lo largo de los episodios de glaciaciones cuaternarias, en los cuales sus plantas hospedadoras se distribuyeron por las montañas de Centroamérica llegando hasta los regiones andinas de Colombia.
18. La fauna de cinípidos en Panamá se encuentra altitudinalmente aislada y bajo una fuerte presión debido a las actividades antropogénicas. Estas poblaciones al estar ubicadas en las zonas más altas del país están amenazadas de extinción debido a los efectos del calentamiento global.

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